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PALEOCENE MULTITUBERCULATES (MAMMALIA, ALLOTHERIA) OF THE ROCHE PERCEE LOCAL FAUNA, RAVENSCRAG FORMATION, SASKATCHEWAN

by

Ⓒ David W. Krause

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
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DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA
FALL, 1976

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled PALEOCENE MULTITUBERCULATES (MAMMALIA, ALLOTHERIA) OF THE ROCHE PERCEE LOCAL FAUNA, RAVENSCRAG FORMATION, SASKATCHEWAN submitted by David W. Krause in partial fulfilment of the requirements for the degree of Master of Science.

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(Supervisor)

D. Gentry Steele

Mark V.H. Wilson

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Date 16 August 1976

ABSTRACT

The discovery of vertebrate fossils in the Paleocene Ravenscrag Formation exposed in the Estevan Coalfield of southeastern Saskatchewan documents the presence of a large and diverse assemblage of multituberculates, an extinct group of prototherian mammals. Multituberculate species of the Roche Percee local fauna identified and described herein include: *Ptilodus* n. sp.; *Prochetodon*, cf. *P. cavus*; *Neoplagiaulax*, cf. *N. hazeni*; *Neoplagiaulax hunteri*; *Mesodma* sp. P; *Mimetodon silberlingi*; *Mimetodon silberlingi*?; *Ectypodus*, cf. *E. powelli*; and *Microcosmodon conus*.

The locality is only the second in the Ravenscrag Formation of Saskatchewan in which fossil mammals have been recovered. Correlation with other fossil-bearing localities in North America provides evidence that beds stratigraphically high in the Estevan Coalfield are of Tiffanian (late Paleocene) age.

The recovery of a nearly complete postcranial skeleton of *Ptilodus* n. sp., the most complete and well-preserved yet known for a multituberculate, permits a reconstruction of its osteology. The postcranium exhibits a structural mosaic of plesiomorphic and apomorphic character states shared, respectively, with cynodonts and prototherians on the one hand, and with therians on the other.

A descriptive and functional analysis of the

postcranial skeleton of Ptilodus n. sp. provides evidence that it was a generalized, non-cursorial, quadrupedal mammal with a flexible vertebral column, long and heavy tail, highly mobile propodial limb segments, and forefeet and hind feet capable of pronation-supination and inversion-eversion, respectively. The locomotory repertoire of Ptilodus is inferred to have been adapted for progression on a discontinuous, spatially irregular and uneven substrate.

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INTRODUCTION

The multituberculates (Mammalia, Allotheria) are an extinct group of prototherian mammals that are common as fossils in late Mesozoic and early Paleogene terrestrial sediments of North America, Europe, and Asia. With one notable exception, the Bear Creek local fauna (Simpson, 1928b, 1929a, b; Van Valen and Sloan, 1966), multituberculates are represented in all well-sampled Late Cretaceous and Paleocene local faunas of North America by an abundance of isolated teeth, but jaws and especially skulls are scarce. Articulated skeletons of allotherians are also very rarely found and their postcranial anatomy is therefore relatively poorly known.

In July of 1971 Miss Roxanne Young of Winnipeg discovered a large, saber-like canine of the pantodont Titanoides in overburden stripped from a lignite mine, now abandoned, near Roche Percee, Saskatchewan. Subsequent discoveries of fossil vertebrates at the same locality (site UAR2) by Dr. G.E. Lammers of the Manitoba Museum of Man & Nature and Miss Young's parents, Mr. and Mrs. B. Young, in 1971, and later, in April of 1972, by the Youngs and myself, indicated that an abundant, diverse, and well preserved thanatocoenosis of Paleocene vertebrates was present.

During the summers of 1972, 1973, and 1974, field parties from The University of Alberta, Edmonton, collected many specimens from the surface and initiated underwater screening operations for the collection of microvertebrate fossils. Fragmentary remains of actinopterygian fishes, frogs, salamanders, turtles, lizards, crocodiles, champsosaurs, birds, and mammals were recovered. Extensive prospecting in the area resulted in the discovery of twelve additional fossiliferous sites, six of which contained specimens in undisturbed strata; however, the majority of specimens was recovered from two sites (UAR2 and UAR2a) located in overburden stripped for mining purposes. One small cutbank (UAR2g) resulting from mining excavations yielded fragmentary but articulated remains of fossil fish _in situ_, and, in August of 1973, a nearly complete and well preserved skeleton of _Ptilodus_. Geographic coordinates of the sites are on file in the Department of Geology, The University of Alberta, Edmonton.

ABBREVIATIONS

Abbreviations used in the text are as follows:

1) Institutions:

AMNH - American Museum of Natural History, New York.

CM - Carnegie Museum of Natural History, Pittsburgh.

MMMN - Manitoba Museum of Man & Nature, Winnipeg.

PU - Princeton University, Princeton.

ROM - Royal Ontario Museum, Toronto.

UA - The University of Alberta, Edmonton.

USNM - United States National Museum, Washington.

2) Locality:

UAR - The University of Alberta, Ravenscrag Formation.

3) Statistics:

CV - Coefficient of variation.

M - Mean.

N - Sample size.

OR - Observed range.

Prob. - Probability.

SD - Standard deviation.

SE - Standard error.

4) Dentitions:

I - Upper incisor.

M,m - Upper or lower molar, respectively.

P,p - Upper or lower premolar, respectively.

5) Vertebrae:

Cd - Caudal vertebra(e).

L - Lumbar vertebra(e).

S - Sacral vertebra(e).

GEOLOGY

The Ravenscrag Formation (Upper Ravenscrag of authors) of southern Saskatchewan and southeastern Alberta, exposed as a broad belt parallel to the International Boundary, "consists of fine sandstones, clays and shales, light-gray to buff with much interbedding and lateral change. Lignite beds, many of them workable coal seams, occur throughout the formation" (Russell, 1950, p.31). The lowest coal seam ('Ferris' or 'No. 1') is traditionally taken to mark the base of the formation (but see Whitaker, 1972).

Russell (1974) has provided a concise summary of previous stratigraphic work, most of which occurred in the southwestern region of Saskatchewan, on the formation. The stratigraphy of the Estevan Coalfield, which lies in the southeastern part of the province and on the northeastern flank of the Williston Basin syncline, has been relatively neglected. McLearn (1930) had early determined that, in southwestern and south-central Saskatchewan, the Ravenscrag Formation was divisible into a lower "grey facies" and an upper "buff facies." Only recently, however, has it been recognized (Broughton, 1972, p.186) that from Big Muddy Valley, in south-central Saskatchewan, to the Estevan region "there is a distinct lithologic change from the grey and buff facies into relatively arenaceous beds."

An extensive survey of the stratigraphy, sedimentology, and paleoecology of the Ravenscrag by the Department of

Mineral Resources, Saskatchewan, under the direction of Dr. P.L. Broughton, is currently in progress. The recent studies of Broughton and his co-workers support earlier conclusions (McLearn, in Fraser et al., 1935) that the strata in which the fossils of the Roche Percee local fauna were recovered are higher in the section than Ravenscrag beds to the west. Preliminary pollen and stratigraphic correlations with strata in North Dakota strongly suggest equivalency with the Tongue River Formation (Broughton, pers. comm., 1976). Correlations across the International Boundary based on evidence provided by fossil mammals must await the descriptions of the local faunas of North Dakota from the Judson, Brisbane, and Riverdale localities by R.C. Holtzman of the University of Minnesota.

Byers (1969, p.333) suggested "that the non-marine Frenchman and Ravenscrag Formations were probably ... derived from Upper Cretaceous and Lower Tertiary rocks and older metamorphic rocks and carbonates to the southwest in Montana." Royse (1971, p.74), on the contrary, has stated that "Paleocene sediments ... entered the Williston Basin from the west and northwest."

The Ravenscrag sediments are fluviatile in origin and were deposited in an alluvial plain environment (McLearn, in Fraser et al., 1935). In the Estevan area, the lower workable coal seams south of Estevan are interbedded with clays and calcareous silts, whereas those stratigraphically higher and to the east (near Roche Percee) are found in predominantly crossbedded sandstones. Holter (1972, p.176) interprets the clays and silts "to represent marginal marine swamp deposits in contrast to the sandstones which indicate a prograding delta facies."

Ravenscrag Formation sediments have been identified as Paleocene by studies of plants (Dawson, 1875; McLearn, 1928 (identifications by W.A. Bell); Berry, 1930, 1935; Bell, 1949, 1965), molluscs (Dowling, 1914; McLearn, 1928, 1929 (identifications by T.W. Stanton); Dyer, in Williams and Dyer, 1930; Russell, 1932b, c, 1940, 1974), and non-mammalian vertebrates (McLearn, 1928 (identifications by C.M. Sternberg); Sternberg, 1932; Russell, 1934; Langston, 1958; Erickson, 1972), as well as by negative evidence supplied by the lack of dinosaur bone above the lowest coal seam. Palynological analyses of Ravenscrag sediments are forthcoming (Broughton, pers. comm., 1975) but Dr. E.B. Robertson, formerly a doctoral student at the University of Minnesota, has found, from a small sample near Roche Percee (site UAR2g), that representatives of *Taxodium*, *Carpinus*, *Ulmus*, *Engelhartia*, *Picea*, *Pinus*, and polypodaceous ferns are present (Robertson, pers. comm., 1973).

More refined dating of Ravenscrag strata is now possible with the recent discovery of several localities bearing vertebrate fossils, including mammals. The localities are as follows:

1) Police Point locality in the Cypress Hills of southeastern Alberta (Krishtalka, 1973);

2) Pine Cree Park locality, near the settlement of South Fork, in southwestern Saskatchewan (Russell, 1974);

3) Unnamed locality near the hamlet of Ravenscrag, in southwestern Saskatchewan, currently being worked by field parties of The University of Alberta; and

4) several sites near the village of Roche Percee, in southeastern Saskatchewan (this paper).

Krishtalka (1973), in his study of the mammals from the Police Point locality, concluded that the Ravenscrag sediments at that level are of Tiffanian age. The fossiliferous beds at Pine Cree Park were determined to have been deposited in Puercan, or, at the latest, early Torrejonian time (Russell, 1974). Identifications of the mammals from the locality near Ravenscrag, Saskatchewan have not been made as yet.

The multituberculates of the Roche Percee local fauna identified and described below document a late Paleocene, or, more precisely, probably a late Tiffanian, assemblage. The strongest faunistic similarity of the multituberculates of the Roche Percee sites is with those recovered from Princeton Quarry, Wyoming, which is currently regarded as being latest Tiffanian in age (Sloan, 1969; Gingerich, 1974b, 1975; Rose, 1975). Detailed biostratigraphic correlation with other Tiffanian localities in the Rocky Mountain region using multituberculates must await R.E. Sloan's monographic revision of the order. Studies of primates (especially Gingerich, 1974b, 1975; Rose, 1975), a group that is abundantly represented in the Roche Percee local fauna, provide a more precise framework for biostratigraphic correlation. An analysis of the primates in the assemblage is in progress.

PART I. MULTITUBERCULATE TAXA OF THE ROCHE PERCEE LOCAL FAUNA

A) DENTAL TERMINOLOGY AND MEASUREMENTS

The terminology and measurements used in describing the dentitions follow Simpson (1929c, p.104; 1937a, pp.73-80), Jepsen (1940, pp.246-262), Clemens (1964, p.30), and Krishtalka (1973, p.4). Measurements were taken with a Bausch and Lomb zoom microscope having a micrometer disc inserted into the ocular, and are expressed in millimeters (mm). Raemakers (1975) has presented a perceptive analysis of errors usually committed in mensuration of small mammalian teeth. Owing to these restrictions, as well as to limitations of the optical equipment at hand, certain measurements (e.g. width of p4) were omitted. In almost all cases only complete teeth, showing no or very little postmortem wear, were employed in measurements. Estimates, necessary because of small sample size, have been noted as such. The enumeration of cusp formulae can also be imprecise. In the case of the internal row of multituberculate M1's especially, the number of cusps listed must be considered as valuations, rather than accurate counts.

The term 'exodaenodont lobe' is used throughout the paper in reference to that portion of enamel on p4 that labially overlies and extends ventrally down the anterior root. This term is not currently in use for multituberculate P4's but was suggested to me by R.C. Holtzman and R.E. Sloan (pers. comm., 1975).

In most ptilodontid and taeniolabidoid species there are three rows of cusps on P4; external, middle, and internal. The number of cusps in each row is given as a formula x:y:z, where x, y, and z designate the number of cusps in the external, middle, and internal rows, respectively. However, in P4's of species of _Ptilodus_ and _Kimbetohia_, there are no cusps present in the internal row (z) and a neomorphic 'row' of cusps is developed labial to the external row (x) on an anteroexternal bulge. The number of cusps in this neomorphic 'row' should not, therefore, be included in the cusp formulae of P4's of the two genera. To do so would obscure the homologies of the cusp rows involved. For example, in P4's of _Ptilodus montanus_ Douglass, 1908, from Gidley Quarry there are 0-3 cusps developed on the anteroexternal bulge, 5-8 in the external row (x), 9-10 in the middle row (y), and an internal row (z) is absent (Simpson, 1937a). The cusp formula for these P4's should be listed as 5-8:9-10:0, not as 0-3:5-8:9-10.

B) METHODS OF IDENTIFICATION

Association of isolated elements of the same taxon is a common and difficult problem to any paleontologist working with microvertebrate samples. Any associations require subjective decisions and are, in essence, working hypotheses that are tested by future discoveries of larger samples and/or more complete material. In this study the following approach was employed:

A. Isolating Discrete Phena

1) As far as possible, complete and well preserved homologous teeth were grouped into discrete phena by microscopic observation.

2) Measurements, as well as cusp or serration counts, were taken.

3) Bivariate scatter plots were made for each tooth position from each site (*e.g.* anteroposterior length and transverse width for all m^1's from site UAR2a) to detect any clustering.

4) Histograms were plotted for each variable from each site, also to detect clustering but, further, to check for any bimodal or multimodal distributions, *i. e.* subclusters within clusters.

5) Outline drawings, using a camera lucida, were made for each tooth position. This method (adapted from Ramaekers, 1975) was applied to all complete and unworn, or slightly worn teeth, which were drawn in occlusal view (molars) or side profile (fourth premolars), and proved effective in visually delimiting the variation in shape and size for each phenon. As Ramaekers emphasized, great care

must be taken to orient each specimen about the same reference points and in exactly the same way.

6) Distinctive qualitative attributes of each phenon were noted (*e.g.* distribution of ridges descending from first serration on p4).

7) Fragments or damaged teeth were allocated to each phenon. Obtainable measurements were added to those taken on complete teeth and incorporated into histograms.

8) Descriptive statistics traditionally employed in studies of mammalian teeth were computed (M, SE, SD, CV).

9) Students *t*-tests were applied to any samples of overlapping or contiguous size ranges from different sites.

B. Association of Phena and Identification of Taxa

1) Three of the multituberculate species from Roche Percee are represented by partially associated material. Associated with the skeleton of *Ptilodus* n. sp. were the lower incisor, p4, m1, P2-4. Jaw fragments containing m1-2 of *Mimetodon silberlingi* (Simpson, 1935a) and p4, m1 of *Mesodma* sp. P were also recovered. Isolated teeth at these positions could therefore be associated in their respective taxa with confidence.

2) Taxa were identified, primarily using fourth premolars, on the basis of diagnoses already in the literature as well as those to be employed in R.E. Sloan's monographic revision of the Multituberculata. Previously known articulated or associated material of the same, or closely related, taxa were utilized, whenever possible, in

the identifications. In all cases, actual specimens, not casts or photographs, were used as comparative material.

3) Size and frequency distributions were used to double-check associations and to allocate previously unknown tooth positions to known taxa (*e.g.* m1 of *Prochetodon* and M1-2 of *Mimetodon silberlingi*).

C) SYSTEMATIC PALEONTOLOGY

Class Mammalia

Subclass Prototheria

Infraclass Allotheria

Suborder Ptilodontoidea

Family Ptilodontidae

Genus *Ptilodus*

Ptilodus kummae, new species

(Figures 1,2; Tables 1-4)

Etymology.- Named for Linda Strong (nee Kumm), who discovered the type specimen and many others.

Type specimen.- UA 9001, a nearly complete postcranial skeleton with associated left lower incisor and P4, right p4, m1, and P2-4.

Type locality.- NW.1/4, sect. 33, Tp. 1, R. 6, W. 2, site UAR2g, Ravenscrag Formation, Saskatchewan.

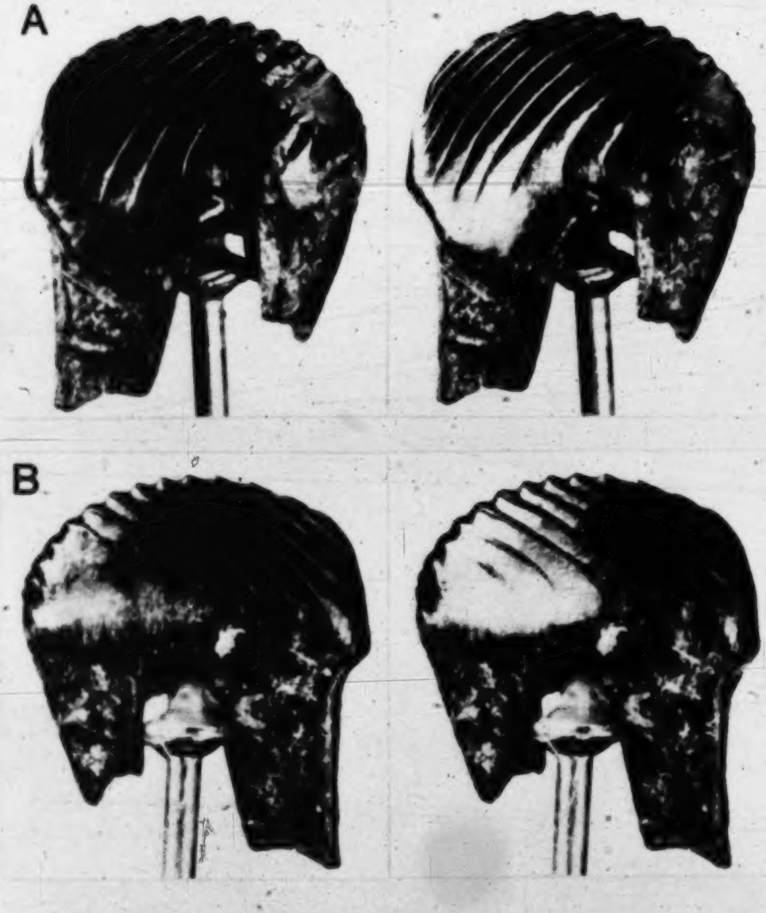
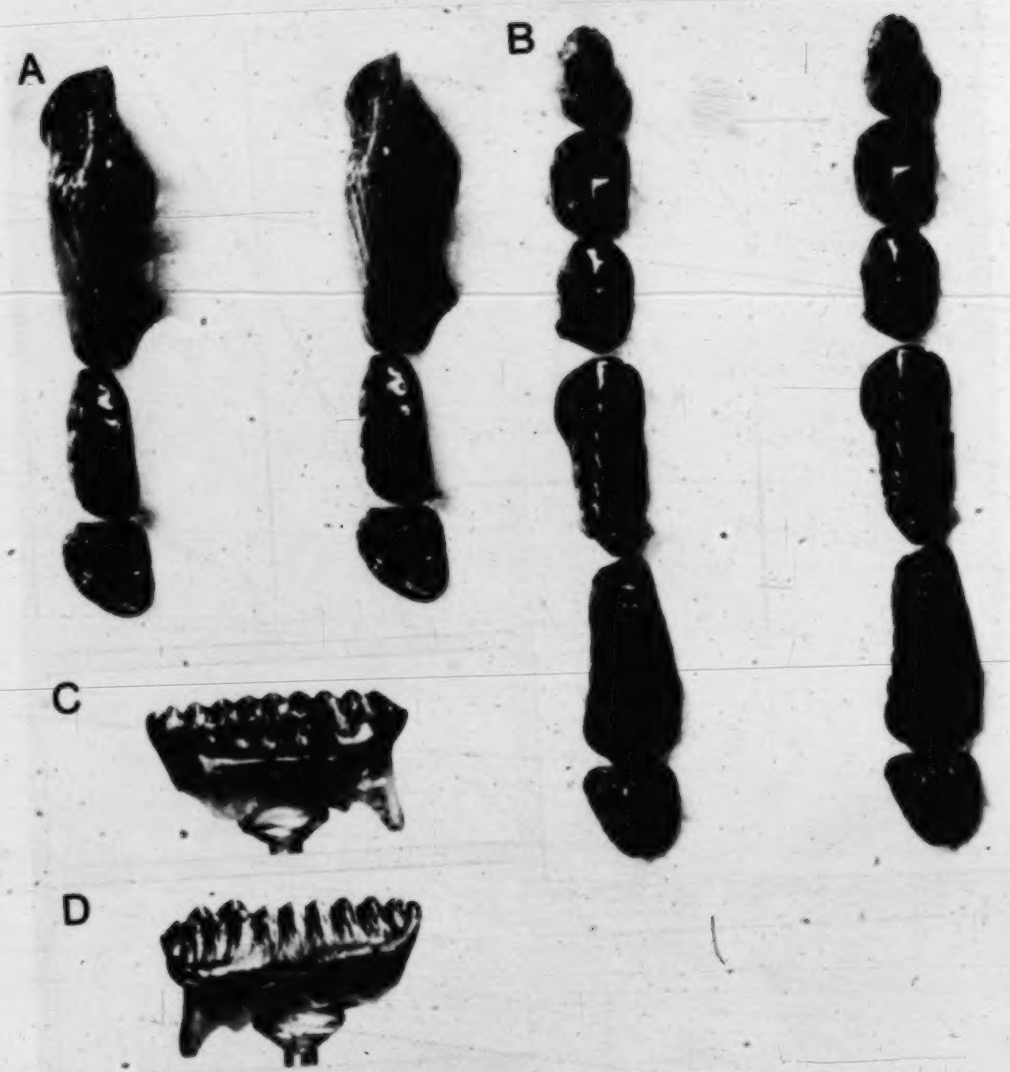

A
B

Figure 2. Ptilodus kummae, n. sp., Roche Percee local fauna, Saskatchewan: (A) occlusal view, stereophotographic pair, composite right lower dentition, UA 10912 (p4 - length 6.8), UA 9001 (m1 - length 3.4), UA 10253 (m2 - length 2.2), about x7; (B) occlusal view, stereophotographic pair, composite right upper dentition, UA 10529 (P1 - length 2.4), UA 9001 (P2 - length 2.4, P3 - length 2.5, P4 - length 4.4), UA 10330 (M1 - length 4.7), UA 9837 (M2 - length 2.2), about x7; (C) labial, and (D) lingual view, UA 9908, left P4, length 5.2, about x7.


A
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C
D

Table 1. Measurements and descriptive statistics of the dentition of Ptilodus kummae, n. sp., Roche Percee local fauna, site UAR2a.

Measurement	N	OR	M±SE	SD	CV
p4 Length	24	6.3-7.3	6.78±.06	.31	4.6
m1 Length	22	3.0-3.6	3.29±.04	.18	5.4
Width	27	1.5-1.7	1.60±.01	.08	4.8
m2 Length	19	2.0-2.5	2.18±.03	.13	6.0
Width	18	1.9-2.1	1.96±.02	.07	3.6
P1 Length	29	2.1-2.8	2.44±.03	.18	7.5
Width	36	1.5-2.0	1.76±.03	.16	9.2
P2 Length	41	2.2-2.9	2.55±.03	.17	6.8
Width	40	1.8-2.4	2.05±.02	.15	7.1
P3 Length	30	2.2-3.0	2.62±.04	.20	7.8
Width	32	1.6-2.0	1.84±.02	.12	6.3
P4 Length	24	4.1-5.5	4.91±.06	.31	6.4
Width	36	1.9-2.6	2.26±.02	.14	6.3
M1 Length	13	4.5-5.2	4.80±.06	.20	4.2
Width	31	2.1-2.3	2.22±.01	.07	3.2
M2 Length	32	1.9-2.5	2.22±.02	.13	5.9
Width	32	1.9-2.5	2.19±.02	.14	6.2

Table 2. Measurements and descriptive statistics of the dentition of _Ptilodus kummae_, n. sp., Roche Percee local fauna, site UAR2.

Measurement	N	OR	M±SE	SD	CV
p4 Length	24	6.3-7.3	6.92±.06	.29	4.2
m1 Length	1	3.3	---	---	---
Width	2	1.6-1.7	1.65±.05	.07	4.3
m2 Width	4	2.2-2.3	2.25±.03	.06	2.6
Length	4	1.9-2.1	2.00±.04	.08	4.1
P1 Length	7	2.2-2.6	2.46±.05	.13	5.2
Width	8	1.8-2.0	1.90±.03	.08	4.0
P2 Length	12	2.3-2.9	2.56±.05	.17	6.8
Width	13	1.9-2.3	2.09±.03	.10	5.0
P3 Length	6	2.5-3.0	2.73±.07	.18	6.4
Width	6	1.8-2.1	1.93±.06	.14	7.1
P4 Length	5	4.5-5.2	4.82±.12	.28	5.8
Width	7	2.2-2.5	2.30±.04	.12	5.0
M1 Length	4	4.6-5.0	4.75±.10	.19	4.0
Width	4	2.2-2.4	2.28±.05	.10	4.2
M2 Length	4	1.9-2.3	2.18±.09	.19	8.7
Width	3	1.9-2.3	2.13±.12	.21	9.8

Table 3. Measurements and descriptive statistics of the dentition of Ptilodus kummae, n. sp., Roche Percee local fauna, site UAR2g.

Measurement	N	OR	M±SE	SD	CV
p4 Length	1	6.6	---	---	---
m2 Length	1	2.3	---	---	---
Width	1	2.0	---	---	---
P4 Length	2	4.7-4.9	4.80±.10	.14	2.9
Width	3	2.1-2.2	2.17±.03	.06	2.7
M1 Length	1	4.4	---	---	---
Width	1	2.1	---	---	---

Table 4. Measurements of teeth of Ptilodus kummae, n. sp., preserved in association with the postcranial skeleton (UA 9001).

Specimen	m1		P2		P3		P4	
	L	W	L	W	L	W	L	W
UA 9001 (right side)	3.4	1.6	2.4	1.8	2.5	1.7	4.4	2.1
UA 9001 (left side)	---	---	---	---	---	---	4.4	2.1

Referred specimens.- p^4: MMMN nos. 335, 564, 565, 572, UA nos. 9751, 9758, 9769, 9773, 9800, 9801, 9853, 9858, 9863-9891, 9912, 9914, 9916, 9922, 9923, 9925, 9949, 9959, 9967, 9968, 9974, 9985, 9986, 9989, 10004, 10089, 10093, 10108, 10117, 10144, 10176, 10231, 10236, 10237, 10246, 10250, 10261, 10262, 10273, 10280, 10289, 10307, 10325, 10326, 10328, 10337, 10341, 10346, 10393, 10405, 10488, 10507, 10517, 10520, 10524, 10553, 10558, 10575, 10576, 10579, 10586, 10596, 10602, 10607, 10610, 10621, 10624, 10628, 10632, 10634-10637, 10639, 10641, 10644, 10645, 10649, 10650, 10662, 10669, 10671, 10676, 10677, 10694, 10708, 10719, 10722, 10731, 10734, 10747, 10750, 10751, 10756, 10758, 10789, 10912-10916, 11293, 11294, 11298, 11307-11316, 11318, 11540-11548, 11550, 11551, 11637, 11638; m1: UA nos. 9777, 9794, 9795, 9805, 9811, 9822, 9857, 9898, 9902, 9907, 10063, 10081, 10082, 10094, 10156, 10172, 10185, 10198, 10209, 10235, 10249, 10284, 10292, 10342, 10369, 10402, 10543, 10626, 10651, 10652, 10740, 11289-11292, 11319-11325, 11554, 11555; m2: UA nos. 9748, 9834, 9892, 9893, 9932, 9958, 10079, 10090, 10128, 10154, 10205, 10227, 10234, 10253, 10283, 10327, 10356, 10414, 10518, 10551, 10600, 10704, 10710, 10894, 11415-11417, 11479, 11480, 11556, 11557; P1: UA nos. 9791, 9816, 9845, 9921, 9936, 9947, 9961-9964, 9966, 9976, 9981, 10011, 10131, 10382, 10391, 10419, 10425, 10437, 10439, 10447, 10450, 10454, 10460, 10467, 10484, 10503, 10529, 10549, 10559, 10560, 10655, 10728, 10748, 11327-11340, 11549, 11552, 11664; P2:

MMMN nos. 354, 370, UA nos. 9812, 9815, 9846, 9855, 9915, 9926, 9927, 9929, 9934, 9935, 9946, 9953, 9956, 9965, 9972, 9973, 10008, 10009, 10012-10014, 10016, 10181, 10380, 10381, 10398, 10401, 10408, 10426, 10428, 10429, 10434, 10436, 10441, 10444, 10448, 10453, 10461, 10464, 10470, 10473, 10474, 10476, 10477, 10479, 10485, 10486, 10493, 10510, 10511, 10555, 10618, 10736, 11341-11354, 11553, 11687-11690; P2 or P3: UA nos. 9848, 11695, 11696; P3: UA nos. 9774, 9832, 9920, 9928, 9930, 9942, 9943, 9948, 9971, 9980, 9990, 10015, 10389, 10400, 10410, 10431, 10435, 10446, 10449, 10451, 10455, 10459, 10462, 10471, 10472, 10475, 10483, 10487, 10497, 10504, 10530-10532, 10545, 10563, 10693, 10733, 11355-11368, 11691-11694; P4: MMMN 331, UA nos. 9827, 9850, 9894-9897, 9899-9901, 9903, 9904, 9908, 9939, 10059, 10072, 10088, 10103, 10119, 10189, 10215, 10239, 10241, 10255, 10256, 10271, 10282, 10285, 10286, 10309, 10332, 10338, 10352, 10354, 10362, 10377, 10427, 10490, 10534, 10569, 10572, 10580, 10601, 10613, 10647, 10661, 10679, 10695, 10703, 10716, 10762, 10773, 10775, 11295-11297, 11369-11386, 11563-11565, 11636, 11639; M1: MMMN nos. 330, 555, UA nos. 9763, 9788, 9798, 9803, 9817, 9819, 9839, 9905, 9906, 10005, 10041, 10064, 10075, 10120, 10173, 10225, 10230, 10274, 10308, 10329, 10330, 10349, 10367, 10388, 10415, 10424, 10568, 10588, 10612, 10625, 10674, 10739, 10763, 10776, 10984, 10991, 11299, 11387-11392, 11394-11404, 11560-11562; M2: MMMN 470, UA nos. 9799, 9837, 9909-9911, 10003, 10050, 10085, 10087, 10096, 10135, 10136, 10139, 10164, 10182, 10187, 10243, 10266, 10303, 10319, 10345, 10383, 10556, 10627, 10749, 11006, 11007, 11405-11414, 11496, 11558, 11559, 11697-11700; humeral fragment: UA 11300; femoral fragment: UA 11301; ulnar fragment: UA 11302.

Sites.- UAR2, UAR2a, UAR2c, and UAR2g, Ravenscrag Formation, Saskatchewan.

Known distribution.- Roche Percee local fauna, Ravenscrag Formation, Saskatchewan; Badwater Creek locality, Shotgun Member, Fort Union Formation, Wyoming (Krishtalka *et al*., 1975); and, questionably, in the Swan Hills local fauna, Paskapoo Formation, Alberta and the Riverdale locality, Tongue River Formation, North Dakota.

Diagnosis.- Smallest of the known species of *Ptilodus* except *Ptilodus douglassi* Simpson, 1935a; angle along anterior margin of crown on p4 (that is, between anterobasal concavity and ventral peak of exodaenodont lobe) more obtuse than in *P. douglassi*; ratio of length of p4: length of m1 greater than in *P. douglassi*; dimensions and ratios as in Tables 1-4; cusp formulae as listed in text; 12-15 serrations on p4 (mode 13).

DESCRIPTION

Lower incisor.- The lower incisor of the type specimen (UA 9001) is incomplete. Preserved is the central part of the tooth; the tips of both the crown and root are broken away. The enamel of the internal face begins much further distally and is considerably thinner than that on the external face. The external face is evenly convex; a distinct, longitudinal ridge marks the junction of the mesial and external faces. The root is elliptical in cross section. Isolated incisors are not assigned.

p4.- The crown is high, symmetrically curved in profile view, and bears 12 (three specimens), 13 (24 specimens), 14 (13 specimens), or 15 (one specimen) serrations. The margin between the anterobasal concavity and the first serration is virtually straight ventrally but curves posteriorly near the first serration. Three ridges (one anterolabially, one medially, and one anterolingually) descend from the first serration. The anterolabial and anterolingual ridges are short and terminate after merging with or approximating the corresponding labial and lingual ridges that descend from the second serration. The medial ridge from the first serration extends ventrally towards the middle of the anterobasal concavity but is deflected labially at approximately halfway along its length and terminates indistinctly at a level horizontal to, or slightly above, the dorsal peak of the anterobasal concavity (in UA 10337 the medial ridge is split and deflected both labially and lingually).

The widths between ridges on the lingual surface increase posteriorly. Lingually, even on unworn specimens, the last three serrations do not bear ridges. The serration anterior to these usually possesses a short lingual ridge, which begins at a point ventral to the serration.

The posterior two or three ridges on the labial surface of the crown are often obscured by wear but appear to have been irregularly spaced and probably anastomosed to some degree. Posteriorly, on the labial surface, a shelf descends from the last serration in an anteroventral direction. The shelf is variably developed and often exhibits wear; however, even on heavily worn specimens, it is never totally obliterated.

The serrations become progressively wider transversely and are relatively blunt posteriorly.

The anterobasal concavity is well defined and deep; on most specimens the most dorsal point is peaked, but on some it is rounded. The enamel labial to the anterobasal concavity extends further ventrally than does the corresponding enamel on the lingual side.

m1.- Cusp formula 6:5. In occlusal view, the anterior edge of the crown is virtually straight; the posterior edge is rounded but is oriented obliquely anterolingually from the posteroexternal corner of the tooth. The external and internal margins of the crown are straight or slightly convex. A slight bulge is usually present labial to and below the second cusp in the external row. On two specimens, UA 10249 and UA 11289, a small cuspule is developed on this swelling, but these are undoubtedly individual variants. The two rows of cusps diverge posteriorly, and are convex dorsally in profile view, the external cusp row being approximately two-thirds the height of the internal one.

The first three cusps in the external row are pyramidal; the last three are subcrescentic. The most anterior cusp in the external row is variably developed but is usually small, being obliterated in heavily worn specimens. In the external row, the cusps usually decrease progressively in size and height anteriorly and posteriorly from the third; in some specimens, however, the ultimate cusp is slightly larger and taller than the penultimate one. The small first and the second cusps are partly joined along their height, as are the fifth and sixth. The third and fourth cusps, by contrast, are relatively isolated from other cusps in the external row. The sixth cusp, unlike other cusps in the row, bears a large, shallow groove on its medial slope.

The cusps of the internal row are large and pyramidal, the third being invariably the largest in that row and highest on the crown. The first and second cusps can be partly joined, the third is isolated, and the fourth and fifth are closely joined, almost to their apices. Small swellings are often present on the ridge descending posterolabially from the fifth cusp in the internal row. On unworn specimens, this ridge is continuous with the ultimate cusp in the external row. On UA 9001, a small accessory cuspule is developed anterior to the first cusp of the internal row. Other specimens show a small swelling in this position. The third, fourth, and fifth cusps, and occasionally the second, each bear one or two vertical grooves on their medial surfaces. These grooves are commonly effaced by wear, especially anteriorly. Heaviest wear on the crown occurs on the medial surfaces of the anterior cusps in the external row.

m2.- Cusp formula 4:2. The crown is longer than it is wide. Both the anterior and labial margins of the crown are virtually straight and perpendicular to one another. The posterior edge, however, is oriented obliquely anterolingually from the posteroexternal corner and merges imperceptibly with the strongly convex lingual edge. The first three cusps of the external row are similar in size and height and are crescentic. The fourth cusp is closely joined to the third and may or may not have a distinct apex. A ridge, which begins from the apex of the third cusp, extends posteriorly along the fourth cusp and then anterointernally to the apex of the second cusp of the internal row. The labial surface of the outer row of cusps is smooth, but the medial face is marked by numerous vertical grooves, both separating the cusps and, especially posteriorly, on the cusps themselves.

The two cusps of the internal row are much larger and have broader bases than those of the external row. The first cusp is larger and higher than the second. It is quadrate in occlusal outline, subcrescentic to crescentic in horizontal section, and bears a deep, vertical groove (occasionally two) on its valley-facing surface. The second cusp, well separated from the first, is triangular, pyramidal, and bears two vertical grooves labially. A small swelling is present posterior to the second cusp of the internal row in approximately one-half of the specimens and, in these cases, a small groove separates the two. Wear is heaviest on the labial surface of the internal row of cusps and along the furrow between the two rows of cusps.

P1.- All specimens of P1 have three main cusps on the crown, one anterior and two posterior. The anterior cusp is slightly smaller and lower than the two posterior ones, which are subequal in size and height. The anterior margin of the crown is convex, the labial and lingual sides are slightly constricted at mid-length, and the posterior edge is straight, being oriented moderately anterolabially from the posterointernal corner of the tooth.

All of the cusp slopes facing the center of the crown are smooth, but on almost all other surfaces the enamel is wrinkled to some degree. The posterointernal cusp is pyramidal and triangular in cross section; the remaining two cusps are lenticular, the anterior one being oriented anterointernal-posteroexternally along its longitudinal axis and the posteroexternal one lying in a more oblique orientation.

P2.- All P2's here referred have four cusps subequally spaced in a square on the coronal surface. One specimen, UA 10426, bears a small accessory cuspule immediately anterior to the anteroexternal cusp. The labial, lingual, and posterior margins of the crown are usually concave in occlusal view, although in any specimen either one or more of these sides can be straight or slightly convex. The posterior margin extends posterolingually from the labial edge of the crown. The anterior border of the tooth is convex.

The enamel on the crown is wrinkled peripheral to the center-facing surfaces of the four main cusps.

The two internal cusps are triangular in horizontal section; the outer two are lenticular.

P3.- The number of cusps can be either four, five, or six (mean 4.76; mode 5). There are in all cases, four main cusps subequal in height and equidistantly spaced in a square about the center of the crown.

The crown, in occlusal view, is irregularly ovate, being wider anteriorly. As in P1 and P2, the valley-facing surfaces of the cusps are smooth, the outer faces wrinkled.

P4.- Cusp formula 5-7:8-10:0 (mode 6:9:0). The outline of the crown, in occlusal view, is approximately an isosceles triangle with the base being anterior. The triangle is disrupted by an anteroexternal bulge on which the enamel is papillate or wrinkled, and which occasionally bears from one to three small cusps or cuspules.

The cusps in the external row are arranged in a gentle arc, convex labially, and are conical, although, at least anteriorly, each often possesses one crest running anteriorly and one posteriorly from base to apex. The cusps extend from the anterior border posteriorly to a level opposite the antepenultimate or penultimate cusp of the medial row. The second cusp is usually largest in the external row. Small cuspules are often interspersed between the main cusps of the external row.

The middle row consists of cusps of subequal height and size, and similar shape, arranged in a nearly straight line. The cusps are joined along their height almost to their apices.

The enamel is smooth about the basal borders of the crown but is wrinkled on the cusps themselves.

Few of the P4's show much wear, but evidence of slight wear exists along the apices of the cusps posteriorly on the medial row and along the lingual face of the crown.

M1.- Cusp formula 7-8:8-11:4-8 (mode 8:9:6). The posterior border of the crown is rounded in occlusal view, whereas the anterior end is straight and oriented anterointernal-posteroexternally. In side profile the coronal surface is concave dorsally.

The cusps of the internal row are variable in number and development. They are largest and highest posteriorly, and decrease in size and height anteriorly. The relatively large, distinct posterior cusps gradually become less distinct anteriorly and form a papillate ridge, which, on unworn specimens, extends to the anterior end of the crown. Wear may abbreviate this ridge considerably.

The cusps of the middle row are quadrate and subcrescentic, the ultimate cusp being the tallest on the crown and the antepenultimate the largest in bulk. Irregularly developed small grooves and ridges are evident on the labial and lingual sides of the cusps on the middle row of unworn teeth. Even slight wear tends to obliterate these structures.

The penultimate cusp is usually the largest and tallest in the external row. The pyramidal cusps of the external row are smooth labially but bear ridges and grooves on their medial faces that are more prominent than those on the cusps of the middle row.

Wear is heaviest on the anterolingual surface of the crown.

M2.- Cusp formula 1:3:3-4 (mode 1:3:3). The occlusal surface of the crown is concave anteriorly and convexly rounded posteriorly. The transverse width of the crown decreases posteriorly.

The single cusp in the external row is the lowest and smallest on the crown. From it, one ridge extends posteriorly to the base of the ultimate cusp of the middle row and then ventrally to its apex. Another ridge passes lingually from the external cusp to the first cusp in the middle row, across its apex to the lingual base of the cusp.

The three cusps of the middle row are well separated from one another. The first is low and transversely elongate. The second cusp is pyramidal to subcresentic, tallest on the crown, and slightly curved anteriorly. The ultimate cusp is subcrescentic and is more curved than the second. Either or both of the last two cusps can possess grooves on their lingual surfaces.

The internal row has three or four pyramidal cusps of subequal height that bear ridges and grooves on their basal medial surfaces. The cusps are closely approximated and joined to about two-thirds of their height.

DISCUSSION

The characteristic shape and cuspidation of P4 and the comparatively symmetrical lateral profile of p4 are apomorphic features shared by the specimens described above and those of the known species of Ptilodus.

According to Sloan (in Van Valen and Sloan, 1966, fig. 4), there are at least six species of Ptilodus: an undescribed species from the Puercan, P. ferronensis Gazin, 1941, from the basal Torrejonian Dragon beds of Utah, P. mediaevus Cope, 1881, P. montanus, and P. wyomingensis Jepsen, 1940, from the Torrejonian of New Mexico, Montana, and Wyoming, respectively, and another undescribed species, Ptilodus sp. A from the Tiffanian. Krishtalka (1973) and Schiebout (1974) extended the stratigraphic ranges of P. montanus and P. mediaevus respectively, into the Tiffanian, but both of these extensions are based on inconclusive evidence. The known species of Ptilodus are remarkably similar to one another. Traditionally, the three broadly contemporaneous species, P. mediaevus, P. montanus, and P. wyomingensis, have been separated by the numbers of serrations on p4, the ranges of which overlap in all three species (Simpson, 1937a; Jepsen, 1940), and by the frequency of occurrence of cuspules on the anteroexternal bulge of P4, being "generally present" in P. mediaevus, "usually lacking in P. montanus", and "absent from PU 14468, the only described P4 of P. wyomingensis" (Krishtalka, 1973, p.9). Obviously, a species assignment using these two characters requires an adequate sample to give some indication of the ranges of variability. Furthermore, numerous P4's of P. wyomingensis since collected from Rock Bench Quarry (PU collections) bear from zero to three cuspules anteroexternally (the same range of variation as is known for *P. montanus* and *P. kummae*) and have a combined cusp formula of 5-7:8-9:0 (personal observation). Specimens of *Ptilodus*, or near *Ptilodus*, but of indeterminate specific affinities, have been recovered from several additional Paleocene localities in the Rocky Mountain region (L.S. Russell, 1932a; Gazin, 1956a, b, 1969; Dorr, 1958; Keefer, 1961; Krishtalka *et al.*, 1975). Plainly, monographic revision of the genus is needed.

In corresponding parts of the dentition, *P. kummae* can easily be differentiated from *P. ferronensis* and *P. mediaevus*, as well as from *Ptilodus* sp. A (Sloan, pers. comm., 1975), by its relatively small size. *P. montanus* and *P. wyomingensis* are closer to *P. kummae* in size; however, application of Student's *t*-test to lengths of p^4 in the three samples results in a probability of <.001 that *P. kummae* is conspecific with either of the former two species. Further, application of the Mann-Whitney U test, using the number of serrations on p^4 to compare samples of *P. kummae* with *P. montanus*, indicates that the differences are significant (0.01>Prob.>0.001). The same result obtains on comparison of *P. kummae* with *P. wyomingensis*.[1]

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[1] Data for the above statistical tests were derived from Simpson (1937a) and Simpson *et al.* (1960) for *P. montanus* and from Jepsen (1940) for *P. wyomingensis*.

Ptilodus kummae is most similar to ?*Ptilodus douglassi*, a species known from the Torrejonian Gidley and Silberling quarries of Montana (Simpson, 1935a, 1937a) and from locality 40147, Black Peaks Formation, Texas (Schiebout, 1974). In 1966, Sloan (in Van Valen and Sloan, fig. 5) transferred ?*P*. *douglassi* to *Mimetodon*, but, more recently, he (pers. comm. to Schiebout, 1974) placed the species in *Neoplagiaulax*. Specimens collected by the American Museum of Natural History since Simpson's publications (1935a, 1937a) include six teeth (four p4's and two P4's) that are probably referable to this form, and the opportunity is taken here to illustrate (Fig. 3A-E) and list measurements (Table 5) of them.

"The ratio between lengths of p4 and m1 normally ranges from 1.4 to 2.0" in neoplagiaulacids (Sloan and Van Valen, 1965, p.221); ?*P*. *douglassi*, with a ratio of 1.76, was presumably placed in the Neoplagiaulacidae for this reason. This ratio, however, is not as clear-cut between neoplagiaulacids and ptilodontids as was originally thought. For instance, in both *Neoplagiaulax macrotomeus* (Wilson, 1956), and *Ptilodus kummae* the ratio is 2.05 (the ratio for *P*. *kummae* was computed from the means of the lengths of p4 and m1 in the large Roche Percee sample). Apart from the low ratio of p4:m1 in ?*P*. *douglassi*, there appears little quantitative or qualitative reason to separate ?*P*. *douglassi* and *P*. *montanus*. The lengths of p4 in the two samples do not overlap but are contiguous and, when combined, show a CV of

Figure 3. *Ptilodus douglassi*, Gidley Quarry, Montana: (A) labial, and (B) lingual view, AMNH 35515, right p4, length 6.8, about x9; (C) labial, (D) lingual, and (E) occlusal view, stereophotographic pair, AMNH 35514, right P4, length 4.4, about x9. *Ptilodus kummae*?, Swan Hills local fauna, Alberta: (F) occlusal view, stereophotographic pair, UA 11999, right M2, about x9. *Ptilodus kummae*, Badwater Creek locality, Wyoming: (G) occlusal view, stereophotographic pair, CM 16134, P3, length 2.5, about x8.

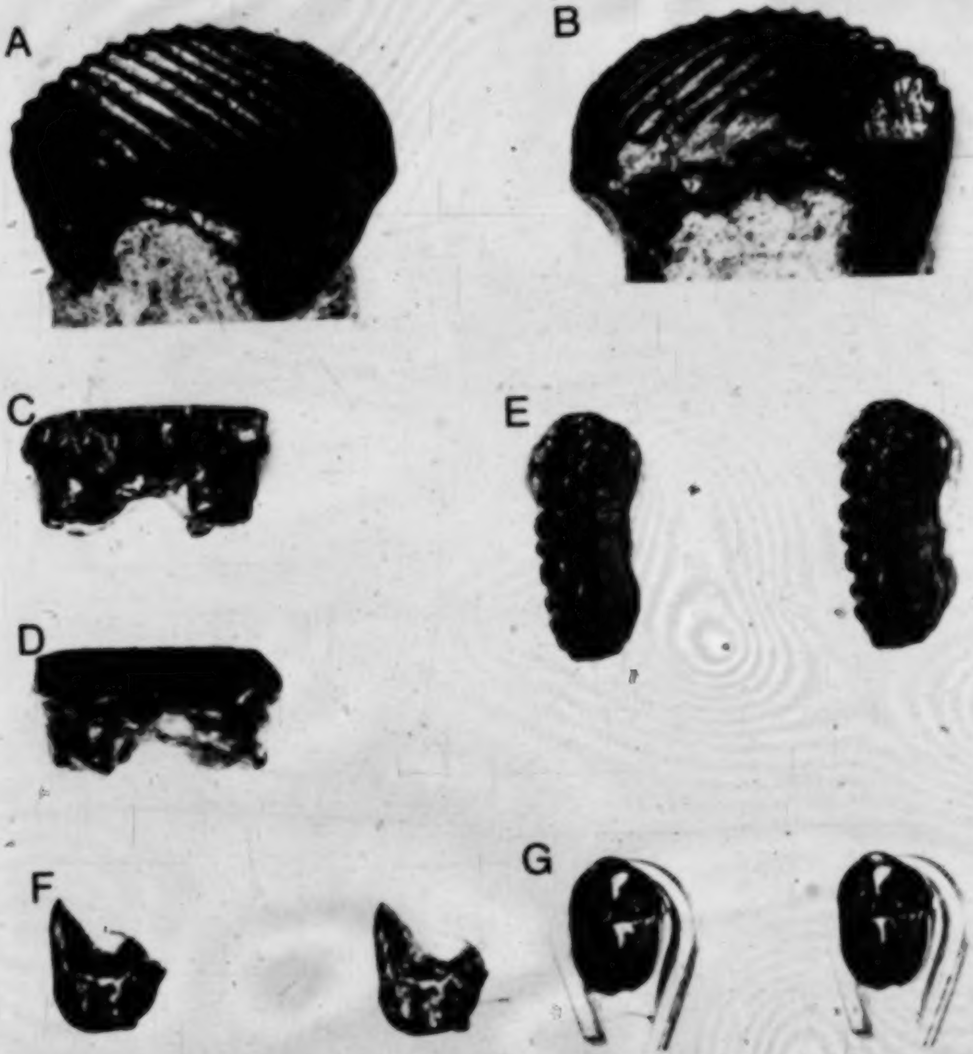
A
B
C
E
D
F
G

Table 5. Measurements and cusp formulae or serrations of fourth premolars of _Ptilodus douglassi_, Gidley Quarry, Lebo Member, Fort Union Formation, Montana.

Specimen	Length	Width	Cusp formula or serrations
AMNH 35511 - p4	6.3	---	12
AMNH 35513 - p4	6.9	---	12
AMNH 35515 - p4	6.8	---	13
AMNH 35516 - p4	6.7	---	13
AMNH 35512 - P4	4.4	2.1	6:7:0
AMNH 35514 - P4	4.4	2.2	8:9:0

6.8.[1]

The two P4's, AMNH 35512 and AMNH 35514, are smaller than those of P. montanus, thereby correlating well with the size of p4's of ?P. douglassi, and are probably correctly referred to the latter species. If so, the species can be assigned to Ptilodus with little doubt. The two P4's, as in other species of Ptilodus, are low, do not rise posteriorly, have many cusps in the external row, and exhibit an anteroexternal bulge with or without cusps (AMNH 35514 has a single cusp and AMNH 35512 has none). Further, P. douglassi is larger than and has fewer cusps on m1 than any species of Neoplagiaulax. As such, in all known features of its dentition, P. douglassi appears to be correctly placed in Ptilodus; the low ratio of the lengths of p4 to m1 should be used as a criterion diagnostic of the species (if, indeed, it is distinct from P. montanus) and not to separate it from the genus.

This assignment creates further problems in that, in terms of size, serration counts, and cusp formulae, P. kummae and P. douglassi cannot be easily distinguished. However, relative to p4's of P. kummae, those of P. douglassi are lower and have a more convex and sloping anterior margin (compare Fig. 1A,B with Fig. 3A,B). The anterior margin of p4 in P. kummae rises relatively sharply and, near the first serration, bends posteriorly. The different ratios between lengths of p4 and m1 is the most distinctive criterion separating these two species.

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[1] Data for P. montanus from Simpson et al. (1960, p.40).

Krishtalka _et_ _al_. (1975) described specimens of _Ptilodus_ from the Tiffanian Badwater Creek locality of Wyoming. Krishtalka (pers. comm., 1975) agrees that these specimens are referable to _P_. _kummae_. Several of the Badwater specimens, however, pertain to _Prochetodon_ (see below). Furthermore, two specimens (CM 16134 and CM 16129) are P3's (see Fig. 3G), not P2's of _Ptilodus_, as Krishtalka _et_ _al_. (1975) indicated.

Also probably referable to _P_. _kummae_ is a P4 (UA 5645) from the Swan Hills local fauna, Alberta, which Krishtalka (1973) described and figured, along with specimens from the Police Point locality, and allocated to _P_. _montanus_, and a fragment of M2 (UA 11999), collected in 1972 by D. O'Brien, which I estimate to have measured 2.4 (length) by 2.3 (width) mm (see Fig. 3F). The measurements of UA 5645 suggest closer affinities with _P_. _kummae_ than with _P_. _montanus_, but the evidence is inconclusive and a decision must await the recovery of a larger sample from the Swan Hills. L.S. Russell (1967), in his treatment of the Swan Hills local fauna, did not refer any specimens to _Ptilodus_.

In 1962, a Field Museum of Natural History expedition recovered three isolated teeth (p4, P1, P3) of a small species of _Ptilodus_ from the Riverdale locality in the

Tongue River Formation of North Dakota (Holtzman, pers. comm., 1975). All three teeth are structurally similar to, and fall within the limits of size variation of, homologous teeth of _P_. _kummae_ in the Roche Percee sample. Holtzman is preparing a thorough description of the mammalian fauna from the Riverdale locality, which is now submerged beneath approximately 50 feet of water in the Garrison Dam Reservoir.

Simpson (1937a, p.87) found that the sample of P3's of _P_. _montanus_ exhibited a great degree of variability in length (CV=18.5) and cusp number (four to seven) and concluded that P3 was "in the process of reduction and that its great variability is a feature of degeneration," as had Granger and Simpson (1929) earlier. Various authors (_e_._g_. Jepsen, 1940; Clemens, 1964) have since accepted that the P3 is exceedingly variable. Using data from Simpson _et al_. (1960, p.66) for _P_. _montanus_, it was found that Simpson had made an error in calculation; the CV for the length of P3 of _P_. _montanus_, based on the parametric mean and standard deviation, is 6.2, not 18.5 (using sample statistics, the CV is 6.4). The lengths of the anterior upper premolars in the sample of _P_. _kummae_, including that of P3, show CV's of between 5.2 and 7.8, well within the range expected for a single mammalian species (Simpson _et al_., 1960; but see Gingerich, 1974a). Therefore, although different in function, the anterior upper premolars (P1-3) and the more posterior fourth premolars and molars appear to show broadly equivalent amounts of variation in size. The evidence from the large samples of P3 of *P. montanus* and P1-3 of *P. kummae* appears to not strongly support Szalay's (1965, p.9) belief that "the non-grinding and non-occluding three anterior upper premolars of ptilodontids are more prone to variation than are the remaining teeth."

The high variability in the cusp number of P3 (four to seven in *P. montanus*; four to six in *P. kummae*) is, however, still unexplained. The variation is probably not owing simply to the lack of occlusal relations with any corresponding lower premolars. The number of cusps on the non-occluding P1's and P2's of both *P. montanus* and *P. kummae*, for instance, is constant; three on P1, four on P2 (one P2, UA 10426, of *P. kummae* bears a small cuspule anterior to the anterolabial cusp).

It should be noted that the cusps present on the external row of most neoplagiaulacid P4's are not involved in shear with the p4 and probably served the same function as the cusps of P1-3. Novacek and Clemens (in press) suggest that, late in ontogeny, the P4, becoming heavily worn apically, may assume a new role, perhaps functionally extending the crushing action of the molars or coming into occlusal contact with p4. In *Ptilodus*, the function of the anteroexternal cusps of P4 is augmented by the presence of two rows of cusps labial to the middle row. The first external row of P4 in *P. montanus* has five to eight cusps

(Simpson, 1937a); in P. kummae, as in P. wyomingensis (personal observation), five to seven are present. In all three species, the anteroexternal bulge (the second external 'row') bears zero to three cusps or cuspules. Therefore, although most students (e.g. Abel, 1912; Simpson, 1926; Clemens, 1962, 1964; Szalay, 1965; Novacek and Clemens, in press) believe that the anterior upper premolars served to grasp, secure, and orient the bolus of food prior to its posterior migration to the shearing premolars, it appears that P1 and P2 in Ptilodus, being the first teeth to encounter the food after the incisors, were more important in these functions and consequently are more conservative in coronal construction. The cusps of P3 and those developed labial to the middle row of P4 are more variable in number, perhaps implying that these cusps were functionally less critical than those developed on P1 and P2 and were therefore not maintained in constant numbers by stabilizing selection. One could also argue, however, as, for instance, has Van Valen (1965, p.386), that variation is maintained "by adaptation to different parts of a niche." Although that possibility may exist for the variable number of cusps on P3 and, anteroexternally, on P4, such an inference would be entirely speculative.

Genus Prochetodon

Prochetodon, cf. P. cavus Jepsen, 1940

(Figure 4; Tables 6,7)

Referred specimens.- p4: MMMN 523, UA nos. 9830, 9919, 9979, 10036-10040, 10060, 10098, 10106, 10305, 10317, 10397, 10421, 10542, 10565, 10583, 10619, 10640, 10643, 10659, 10729, 11304-11306, 11317, 11537, 11538; m1: UA nos. 9796, 10053, 10095, 10124, 10161, 10622, 10768, 11326, 11418, 11419, 11539; P1: UA nos. 10390, 10433, 10465, 10482, 11420; P2: UA nos. 9753, 9825, 9960, 9975, 10417, 10432, 10442, 10523, 10668; P3: UA nos. 9991, 10017, 10386, 10409, 10557, 10584, 10730, 11303; P4: UA nos. 10194, 11450.

Sites.- UAR2 and UAR2a, Ravenscrag Formation, Saskatchewan.

DESCRIPTION

p4.- This tooth bears 15 or 16 serrations.[1] The lingual surface exhibits 13 ridges; the labial surface has 14 (three specimens) or 15 (one specimen). The height of the first serration above the anterobasal concavity is approximately

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[1] These numbers are considerably higher than the 12 or 13 listed by Jepsen (1940) for P. cavus but, from his fig. 5 (pl. IV) and from an earlier discussion (1930b, p.510), it appears he chose to not count the serrations posterior to those giving rise to ridges, or, that his specimens were too worn to observe the posterior serrations. My observation of PU 14436, at least, indicates that the latter was probably the case.

Figure 4. *Prochetodon*, cf. *P*. *cavus*, Roche Percee local fauna, Saskatchewan: (A) labial, and (B) lingual view, MMMN 523, left p4, length 8.0, about x9; (C) occlusal view, stereophotographic pair, UA 10622, right m1, length 4.1, about x8; (D) occlusal view, stereophotographic pair, composite left upper dentition, UA 10433 (P1 - length 2.3), UA 10432 (P2 - length 2.6), and UA 10584 (P3 - length 3.5), about x9; (E) labial, (F) lingual, and (G) occlusal view, stereophotographic pair, UA 10194, right P4, length 5.5, about x8.

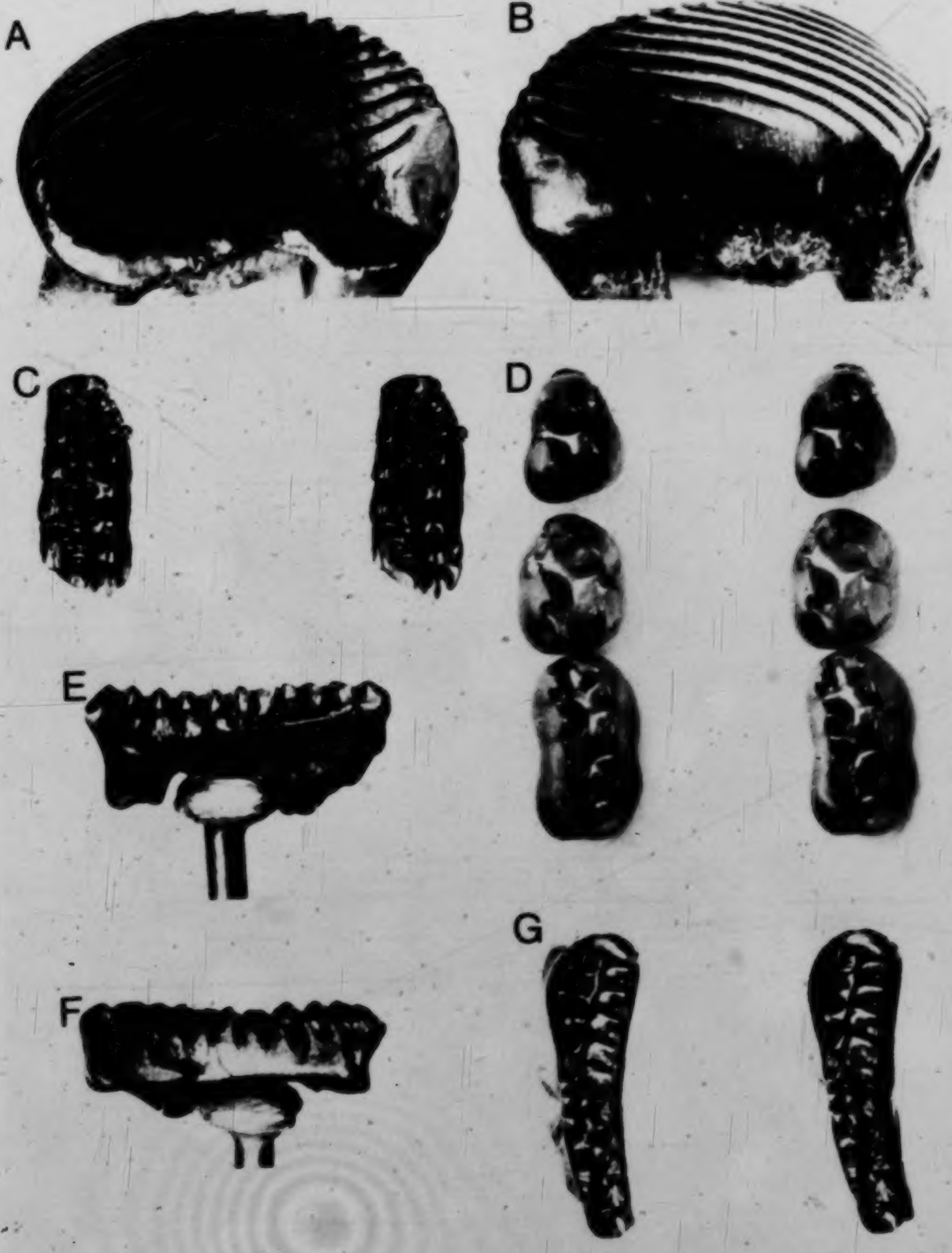
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Table 6. Measurements and descriptive statistics of the dentition of Prochetodon, cf. P. cavus, Roche Percee local fauna, site UAR2a.

Measurement	N	OR	M±SE	SD	CV
p4 Length	2	8.1-8.2	8.15±.05	.07	0.9
m1 Length	5	3.5-4.2	3.88±.13	.29	7.4
Width	5	1.6-1.9	1.76±.05	.11	6.5
P1 Length	5	2.1-2.3	2.18±.04	.08	3.8
Width	5	1.7-1.9	1.82±.04	.08	4.6
P2 Length	7	2.5-2.8	2.61±.04	.11	4.1
Width	7	2.0-2.2	2.11±.03	.09	4.2
P3 Length	4	3.5-3.7	3.55±.05	.10	2.8
Width	4	2.0-2.2	2.08±.05	.10	4.6
P4 Length	1	5.5	---	---	---
Width	1	1.8	---	---	---

Table 7. Measurements and descriptive statistics of the dentition of *Prochetodon*, cf. *P. cavus*, Roche Percee local fauna, site UAR2.

Measurement	N	OR	M±SE	SD	CV
p^4 Length	1	8.0	---	---	---
P2 Length	2	2.7-2.8	2.75±.05	.07	2.6
Width	2	2.1-2.2	2.15±.05	.07	3.3

one-half the length of the tooth. The margin between the ventral apex of the exodaenodont lobe and the first serration is smoothly arcuate in lateral view. The crown is arched far posteriorly and the posterior slope, although convex, is consequently almost vertical. The exodaenodont lobe does not extend far ventrally, as it does in Ptilodus, and is gently rounded along its base. In lateral profile, therefore, the crown closely approximates the shape of a kidney with the hilux of the kidney situated between the two roots.

The roots, compared to those of Ptilodus, are relatively small and slender. A low, bulbous interradicular crest is present between the two roots.

m1.- Cusp formula 7-8:5 (mode 8:5). The posterior margin of the crown is slightly convex and oriented anterointernal-posteroexternally; anteriorly, the margin of the tooth is almost straight. The lingual and labial edges are straight to slightly convex and converge anteriorly. The anterior portion of the crown overhangs the anterior root.

The cusps of the external row are four-sided, the first five being pyramidal, the last three subcrescentic. The cusps progressively decrease in size anteriorly from the fifth (when eight cusps are present); the last three are subequal in size and are slightly smaller than the fifth. A small, pointed cuspule occurs ventral and labial to the junction of the third and fourth cusps of the external row on UA 10622, but surely represents an individual variant.

The first four cusps of the internal row are subequal in height but increase in bulk posteriorly. The fifth and ultimate cusp is lower than the preceding four but is the largest in size.

The prominent ridges and grooves on the valley-facing surfaces of the cusps of both rows are present as on the m1's of most ptilodontoid genera, but, in addition, the m1's of Prochetodon also possess shallow ridges and grooves on the outer surfaces of these cusps, especially on those of the external row.

P1.- The crown of P1 is triangular in occlusal outline, with one anterior and two posterior cusps. The anterior cusp and the posteroexternal cusp are similar in shape, both being tall and each bearing a crest oriented anterointernal-posteroexternally and extending from base to apex. The posterointernal cusp is relatively low and conical and bears an indistinct crest, oriented perpendicular to those on the other two cusps.

P2.- Four large cusps dominate the crown of P2. The anterointernal, anteroexternal, and posteroexternal cusps, arranged in a quarter-circular arc about the posterointernal cusp, are subequal in size and height, and each bears a distinct crest running from base to apex, oriented along the longitudinal axis of the arc. The posterointernal cusp, by contrast, is low, usually three-sided, and nearer the center of the crown than the other three cusps.

P3.- The crown of P3 bears five cusps in the external row and four in the internal row. The rows of cusps are parallel to one another and are convex labially. The crown is subrectangular and is constricted at approximately midway along its length. Each cusp in the external row is elongate anteroposteriorly and lenticular in cross section, bearing a longitudinal crest along its surface. The third cusp is the largest in the row and is not closely joined to those anterior or posterior to it. The first and second cusps are joined to approximately one-half their height and the fourth and fifth to about two-thirds of their height. Small, irregular papillae and vertical wrinkles are present on the labial surface of the external row of cusps.

Low and triangular in cross section, the four cusps of the internal row are situated opposite the junctions of the cusps of the external row. The cusps of the internal row are subequal in size and shape in most specimens; in UA 10584, the ultimate cusp is shorter than any of the preceding three.

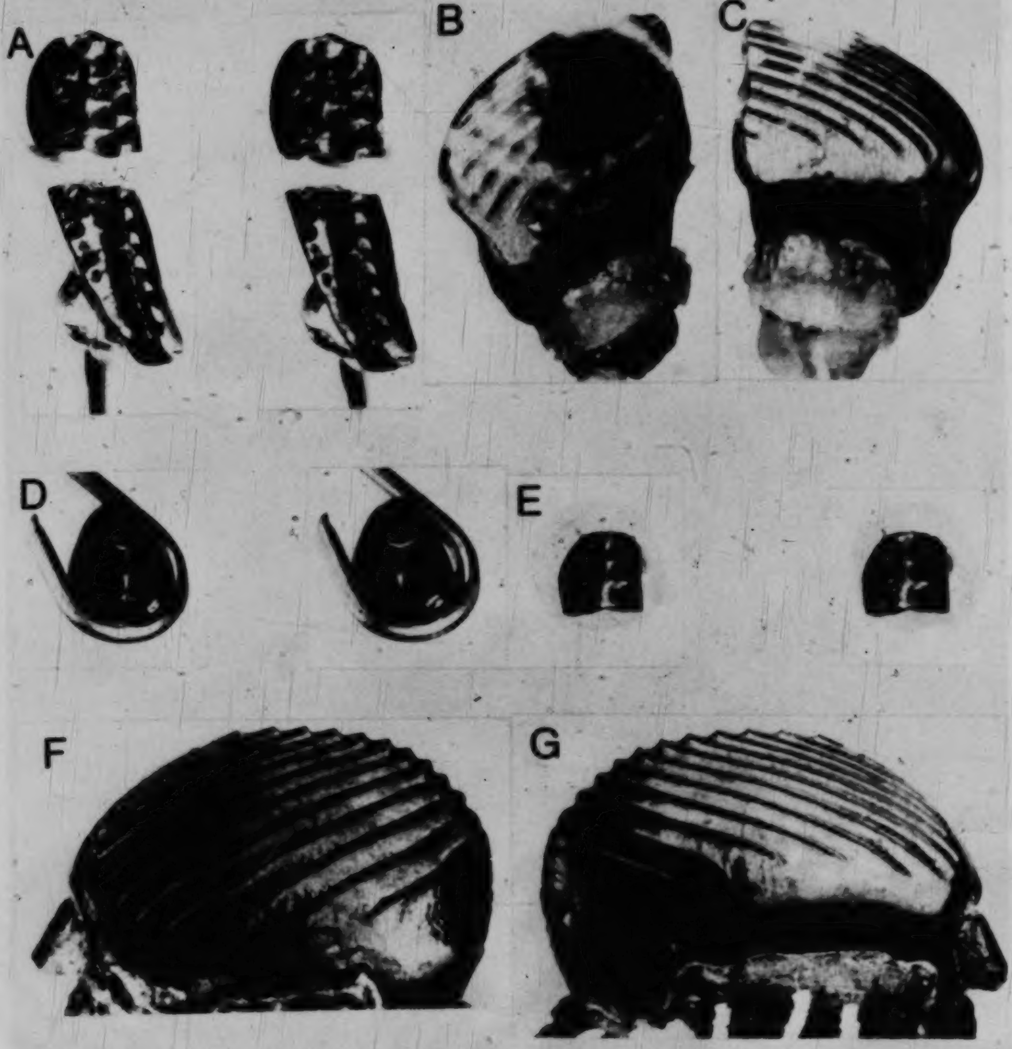
P4.- The single complete specimen (UA 10194) referred here has 11 cusps in the middle row and five triangular or lenticular cusps followed posteriorly by three small conical cuspules in the external row. As in Ptilodus, an internal row of cusps is absent. No papillate or cuspidate anteroexternal bulge, characteristic of P4's of Ptilodus, is developed.

The anterodorsal and posterodorsal corners of the crown on the labial surface are right-angled, giving the crown a rectangular appearance in labial view.

DISCUSSION

Prochetodon has been reported to occur at only two Paleocene localities, both of which are Tiffanian and in North America: Princeton Quarry, Polecat Bench Formation, Wyoming (Jepsen, 1940) and Swan Hills locality 1, Paskapoo Formation, Alberta (L.S. Russell, 1967). The two specimens from the Swan Hills (ROM 05607 and ROM 05608 - both p4's), which Russell referred to Prochetodon sp., are much smaller than any known p4's of Prochetodon and are, in fact, indistinguishable from p4's of Neoplagiaulax, cf. N. hazeni (Jepsen, 1940) from the Roche Percee local fauna and should be transferred to that species. Furthermore, ROM 05603, an m1, and ROM 05606, an anterior fragment of p4, are also referable to Neoplagiaulax, cf. N. hazeni. Russell (1967) referred these latter specimens to Ectypodus cochranensis (L.S. Russell, 1929) (Ectypodus cochranensis has been transferred to Anconodon by Sloan (in Van Valen and Sloan, 1966, fig. 5) and Anconodon sp., respectively. However, fragments of two P4's (UA 11997 and UA 11998 - see Fig. 5A), which D. O'Brien recently collected from Russell's locality

Figure 5. Prochetodon sp., Swan Hills local fauna, Alberta: (A) occlusal view, stereophotographic pair, UA 11998, anterior fragment of right P4, and UA 11997, posterior fragment of right P4, about x8. Prochetodon, cf. P. cavus, Badwater Creek locality, Wyoming: (B) labial, and (C) lingual view, CM 12451, anterior fragment of left p4, about x8; (D) occlusal view, stereophotographic pair, CM 16138, right P1, length 2.3, about x8; (E) occlusal view, stereophotographic pair, CM 23687, anterior fragment of right P4, about x8. Prochetodon cavus ?, Fritz Quarry, Wyoming: (F) labial, and (G) lingual view, PU 17923, left p3,p4, length p4: 7.6, about x8.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1, are undoubtedly referable to Prochetodon, but without better material a definite species assignment cannot be made. I estimate the length of the composite Swan Hills P4 (Fig. 5A) to be about 5.8 mm. The width of UA 11998, an anterior fragment, is 2.0 mm.

The genus is also known from the Wasatchian Willwood Formation, Wyoming (Jepsen, 1940, p.327). McKenna (1960a, p.39) reported the occurrence of two upper premolars of "an undescribed genus and species similar to Prochetodon" from the early Wasatchian of Colorado, but these teeth are structurally quite different from P3's and, especially, P4's of the known species of Prochetodon. A ?P3 from locality 11 of the Porcupine Hills Formation (formerly thought to be in the Paskapoo Formation - see Carrigy, 1970, 1971) near Cochrane, Alberta, which L.S. Russell (1932a) referred to Ptilodus? sp., evoked the comment from McKenna (1960a, p.40), "Whether this tooth represents Prochetodon is not known." This specimen (UA 427) is undoubtedly a P3 of Ptilodus. Its size (length 3.2; width 2.3) and cusp formula (six) are within the range of variation for Ptilodus montanus, but more material is required for specific identification.

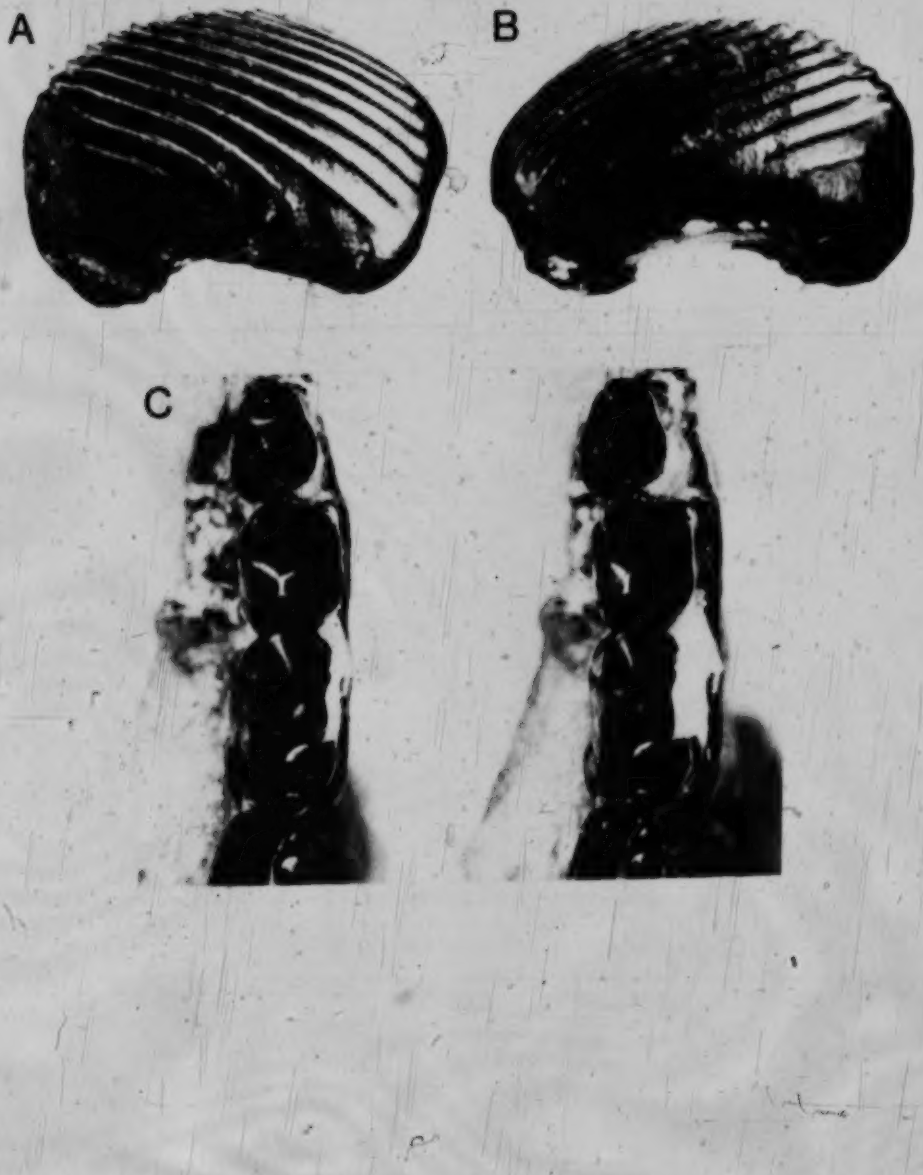
A P3 (CM 16135) from the Tiffanian Badwater Creek locality, Wyoming, which Krishtalka et al. (1975) recognized as resembling P3's of Prochetodon cavus but assigned to Ptilodus sp., is identical to P3's of Prochetodon from Roche

Percee and should therefore be assigned to that genus. Further, an M2 (CM 12454), which those authors also referred to *Ptilodus* sp., should probably also be allocated to *Prochetodon*. If correctly identified, this specimen is the first known M2 of the genus. Its width (2.8 mm) is considerably larger than the width of CM 16165 (2.1), an M1 referred to *Ptilodus* sp., and both of its linear dimensions fall well outside the range of variation of M2's of *Ptilodus kummae* from Roche Percee. Other specimens referable to *Prochetodon*, but which Krishtalka *et al*. (1975) assigned to *Ptilodus* sp. are as follows: CM 12451 (p4 - see Fig. 5B,C), CM 12490 (p4), CM 16120 (p4), CM 23685 (p4), CM 16138 (P1 - see Fig. 5D), CM 16133 (P3, not P4 as listed), and CM 23687 (P4, not m1 as listed - see Fig. 5E).

Molars of *Prochetodon* other than m1 were not recognized in the Roche Percee sample and, in fact, still remain unknown for the genus. Jepsen (1940, p.310), however, noted that an M1 described by Simpson (1936) and an m2 by Simpson (1937b, p.3), both listed as ptilodontid indet., may belong to *Prochetodon*, as may the M2 (CM 12454), which Krishtalka *et al*. (1975) referred to *Ptilodus* sp. (see above). The possibility does exist that m2's, M1's, and/or M2's of the Roche Percee sample of *Prochetodon* were mistaken as large variants of *Ptilodus kummae* although no distinct qualitative or quantitative gaps were noted in the large sample of the latter.

The specimens of Prochetodon from the Roche Percee sites show several minor differences from those of Princeton Quarry, primarily in that they are slightly larger, the anterior margin of p4 is more evenly curved (compare Fig. 4A,B with Fig. 6A,B), the exodaenodont lobe of p4 is less distinctly set off from the rest of the crown, P2 has four, rather than three, cusps (PU 14434, a maxillary fragment from Princeton Quarry, bears a P2 with an incipiently developed anterior cusp), and P3 has, in the external row, five, rather than four, cusps. These differences may be taxonomically significant but, until more specimens are discovered, a formal separation here would be premature. Several specimens recently collected from the Schaff and Fritz Quarries, which are stratigraphically and geographically near the Princeton Quarry (Gingerich, 1974b; Rose, 1975), appear to show characteristics possessed by both the Roche Percee and Princeton Quarry specimens. PU 19369, a left maxillary fragment from Schaff Quarry containing P1-4 (Fig. 6C), has a four-cusped P2 and a P3 with five cusps in the external row. This specimen corroborates Jepsen's (1940) tentative association of P4 with P1-3 of Prochetodon. Lower fourth premolars from the Schaff and Fritz Quarries (PU 19503 and PU 17923 (Fig. 5F,G), respectively) are closer, in size and shape, to those from Princeton Quarry.

Figure 6. Prochetodon cavus, Princeton Quarry, Wyoming: (A) labial, and (B) lingual view, PU 14436, right p4, length 7.5, about x8. Prochetodon cavus?, Schaff Quarry, Wyoming: (C) occlusal view, stereophotographic pair, PU 19369, left P1 (length 2.1), P2 (length 2.4), P3 (length 3.6), and P4 (length 4.6), about x9.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Family Neoplagiaulacidae

Genus *Neoplagiaulax*

Neoplagiaulax, cf. *N. hazeni* (Jepsen, 1940)

(Figure 7A-G; Tables 8-10)

Referred specimens.- p4: UA nos. 9779, 9783, 9802, 9828, 9833, 9844, 9854, 9918, 9933, 9937, 9954, 9987, 9988, 10019-10026, 10061, 10067, 10073, 10100, 10102, 10138, 10146, 10165, 10171, 10188, 10211, 10214, 10219-10221, 10223, 10247, 10257, 10265, 10277, 10336, 10359, 10376, 10489, 10491, 10499, 10500, 10506, 10516, 10526, 10538, 10552, 10566, 10567, 10570, 10581, 10582, 10590, 10595, 10604, 10606, 10617, 10638, 10642, 10660, 10665, 10666, 10672, 10675, 10690, 10691, 10697, 10701, 10705, 10711, 10714, 10721, 10723, 10737, 10754, 10761, 10767, 10784, 10922-10929, 11423-11427, 11566-11573; m1: MMMN 333, UA nos. 9750, 9775, 9818, 9841, 9862, 10071, 10078, 10080, 10110, 10127, 10140, 10141, 10157, 10158, 10167, 10192, 10199, 10202, 10259, 10270, 10281, 10290, 10318, 10320, 10331, 10357, 10358, 10385, 10392, 10395, 10535, 10561, 10562, 10593, 10692, 10713, 10732, 10755, 10765, 10782, 10797, 10903, 10931-10935, 11441, 11443-11447, 11451, 11452, 11574-11576; m2: UA nos. 9804, 9809, 9820, 9826, 10105, 10175, 10179, 10184, 10186, 10260, 10269, 10272, 10275, 10279, 10311, 10322, 10353, 10375, 10404, 10554, 10597-10599, 10683, 10687, 10863, 10995, 10996, 11000, 11466-11474, 11577-11579; P4: UA nos. 9861, 9931, 9969, 9970, 9984, 9992, 9993, 9995, 9996, 9998, 9999, 10028,

Figure 7. *Neoplagiaulax*, cf. *N*. *hazeni*, Roche Percee local fauna, Saskatchewan: (A) labial, and (B) lingual view, UA 10923, right p4, length 5.2, about x8; (C) occlusal view, stereophotographic pair, composite right lower dentition, UA 10593 (m1 - length 3.0), UA 10597 (m2 - length 2.0), about x8; (D) occlusal (stereophotographic pair), (E) labial, and (F) lingual view, UA 10122, left P4, length 3.7, about x8; (G) occlusal view, stereophotographic pair, composite left upper dentition, UA 11599 (M1 - length 4.3), UA 11493 (M2 - length 2.0), about x8. *Neoplagiaulax* *hazeni*, Princeton Quarry, Wyoming: (H) occlusal (stereophotographic pair), (I) labial, and (J) lingual view, PU 14340, left P4, length 4.2, about x8.

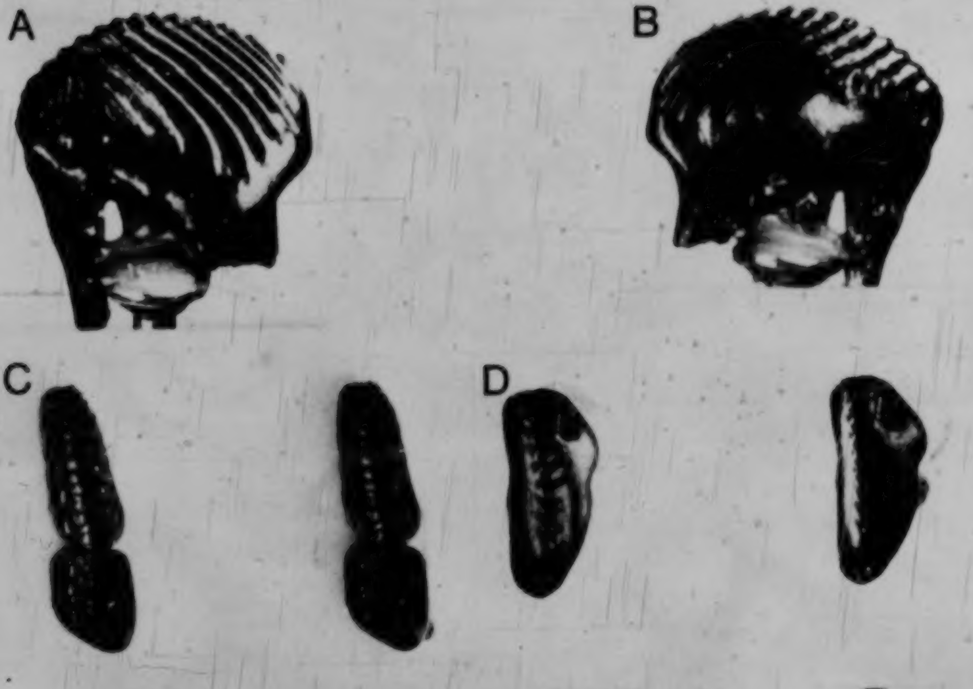
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Table 8. Measurements and descriptive statistics of the dentition of _Neoplagiaulax_, cf. _N._ _hazeni_, Roche Percee local fauna, site UAR2a.

Measurement	N	OR	M±SE	SD	CV
p4 Length	25	4.8-5.3	5.00±.03	.16	3.1
m1 Length	37	2.7-3.2	2.92±.02	.11	3.8
Width	38	1.3-1.5	1.39±.01	.06	4.2
m2 Length	25	1.7-2.1	1.95±.02	.09	4.5
Width	29	1.4-1.6	1.51±.01	.07	4.6
P4 Length	29	3.7-4.2	3.91±.03	.15	3.9
Width	23	1.5-1.8	1.64±.02	.09	5.4
M1 Length	13	3.7-4.3	3.91±.04	.16	4.0
Width	29	1.6-1.9	1.71±.01	.07	3.9
M2 Length	33	1.8-2.1	1.96±.02	.09	4.4
Width	30	1.6-1.9	1.75±.01	.08	4.7

Table 9. Measurements and descriptive statistics of the dentition of Neoplagiaulax, cf. N. hazeni, Roche Percee local fauna, site UAR2.

Measurement	N	OR	M±SE	SD	CV
p4 Length	10	4.8-5.3	5.03±.05	.16	3.2
m1 Length	1	2.9	---	---	---
Width	1	1.3	---	---	---
P4 Length	5	3.6-4.1	3.84±.10	.23	6.0
Width	4	1.5-1.7	1.62±.05	.10	5.9
M2 Length	2	2.1-2.2	2.15±.05	.07	3.3
Width	2	1.8-1.9	1.85±.05	.07	3.8

Table 10. Measurements and descriptive statistics of the dentition of *Neoplagiaulax*, cf. *N. hazeni*, Roche Percee local fauna, site UAR2g.

Measurement	N	OR	M±SE	SD	CV
p4 Length	1	5.3	---	---	---
m1 Length	1	2.8	---	---	---
Width	1	1.4	---	---	---
m2 Length	1	1.8	---	---	---
Width	1	1.5	---	---	---
P4 Length	1	4.2	---	---	---
Width	1	1.8	---	---	---
M2 Length	2	2.0-2.2	2.10±.10	.14	6.7
Width	2	1.8-1.9	1.85±.05	.07	3.8

10029, 10054, 10058, 10068, 10086, 10099, 10101, 10115, 10122, 10155, 10174, 10190, 10370, 10378, 10396, 10422, 10508, 10544, 10564, 10571, 10574, 10592, 10608, 10631, 10633, 10670, 10678, 10684, 10685, 10720, 10727, 10738, 10741, 10746, 10753, 10769, 10771, 10774, 10785, 10956-10963, 11453-11456, 11580-11593; M1: UA nos. 9765, 9768, 9771, 9840, 9814, 9835, 9843, 9859, 9860, 10062, 10065, 10112, 10121, 10123, 10125, 10142, 10195, 10207, 10218, 10276, 10323, 10347, 10348, 10384, 10653, 10657, 10699, 10702, 10706, 10726, 10977, 10985, 10994, 11502-11504, 11521, 11594-11603; M2: UA nos. 9792, 9829, 9938, 10042, 10043, 10091, 10107, 10118, 10145, 10180, 10238, 10248, 10278, 10298, 10301, 10310, 10315, 10364, 10587, 10589, 10752, 10781, 11008-11015, 11481, 11483-11495, 11525.

Sites.- UAR2 and UAR2a, Ravenscrag Formation, Saskatchewan.

DESCRIPTION

p4.- From 13 to 15 (mode 14) serrations are developed on the high, arcuate crown of p4. The height of the first serration above the anterobasal concavity is between one-third to one-half the length of the crown and the height of the crown is slightly less than the length. Three ridges, two anterolabially and one anterolingually, pass anteroventrally from the first serration. The last two to four serrations may bear no ridges at all. Below these serrations vertical crenulations arise both labially and lingually. In about two-fifths of the referred specimens a faint ridge, usually terminating in a swelling, descends ventrolingually from the ultimate serration. The anterobasal concavity is well-defined, deep, and somewhat squared dorsally: p3 was obviously present and has been described (Jepsen, 1940) for _N_. _hazeni_. As in specimens of p4 of _N_. _hazeni_ from Princeton Quarry (PU 14323 and PU 14422), the margin of the enamel between the anterobasal concavity and the ventral apex of the exodaenodont lobe is not straight but rather follows a sinusoidal curve.

A high, interradicular crest abuts the large anterior root, which is triangular in cross section, the most acute angle situated posteriorly. The smaller posterior root is quadrate in horizontal section.

m1.- Cusp formula 8-9:5 (mode 8:5). The apices of the external row of cusps, in occlusal view, follow a labially concave path. The cusps themselves are four-sided, pyramidal anteriorly and crescentic posteriorly, and increase in height from the first to the fourth cusp; posterior to the fourth cusp the cusps are subequal. The cusps of the internal row, much taller than those externally, decrease progressively in height, but not in size, anteriorly and posteriorly from the third (observable only on unworn specimens). The ultimate cusp is invariably the most massive. The first, second, and third cusps are usually joined to about one-half their height, the third and fourth are separated by a deeper trough, and the fourth and fifth are joined to about three-quarters of their height or almost to their apices. All of the internal cusps are flattened and marked by irregular deep vertical grooves on their valley-facing slopes; lingually they are rounded. The ultimate cusps of both rows, which diverge posteriorly, are connected by a long high ridge that is convex posteriorly. UA 10071, an anterior fragment of m1, has an anomalous set of three cuspules developed labial to the fourth, fifth, and sixth cusps of the external row.

m2.- Cusp formula 5-6:3-4 (mode 5:3). All of the cusps of the external row, except the last, are subequal in size and height and are crescentic in horizontal section. The ultimate cusp is generally lower and bears a shallow vertical groove medially. The cusps of the internal row are much larger but decrease in height from anterior to posterior. The second cusp is the smallest in bulk. The first and second are crescentic in cross section; the third is triangular with the apex directed posteriorly. All three are grooved on their valley-facing slopes.

P4.- Cusp formula 1-3:8-10:0 (mode 2:8:0). In occlusal view the crown is gently concave lingually, convex labially but with a large indentation at mid-length, and wider anteriorly than posteriorly. In lateral profile the posterior slope is concave, the anterior slope convex, and the penultimate, antepenultimate, or the fourth from last cusp is tallest on the crown. The anteroexternal cusps, when more than one is present, are larger posteriorly. The enamel overlying the anterior root bulges out and overhangs the root both anteriorly and labially. Rudiments of both the posterobasal and posterolingual basal cusps are developed.

M1.- Cusp formula 7-9:10-13:5-7 (mode 8:12:6). Determination of the number of cusps in the internal row is difficult and may well be inaccurate. The cusps are discrete posteriorly but, at about mid-length, blend into a continuous ridge that, in unworn specimens, can extend to the anterior margin of the crown. Furthermore, unlike Jepsen (1940), I have not counted the raised rim on the anteroexternal corner of the crown as a discrete cusp belonging to the external row and, therefore, have obtained a lower cusp formula.

In lateral aspect, the crown is concave dorsally; in occlusal view, it is concave labially and convex lingually. All of the cusps of the external row are flattened and grooved medially, rounded and oftentimes wrinkled labially, and subequal in size and height, except for the terminal cusp, which is small, low, and closely attached, sometimes indistinguishably, to the penultimate cusp. The cusps of the middle row are four-sided and become progressively larger and more crescentic posteriorly.

M2.- Cusp formula 1:3-4:4-6 (mode 1:4:5). The M2's generally have a higher length:width ratio than those referable to other species represented in the local fauna.

The first and second cusps of the internal row are subequal in height, although wear tends to reduce the first sooner than the second, whereas those following are progressively shorter. The cusps of the middle row are crescentic and larger, and are generally subequal in height. The single cusp of the external row is not a discrete cusp but is an anteroexternal extension of the raised rim of enamel connected to the apices of both the first and last cusps of the middle row.

DISCUSSION

Jepsen (1940) originally described Ectypodus hazeni (now assigned to Neoplagiaulax (Sloan, in Van Valen and Sloan, 1966, fig.5)) from Princeton Quarry in the Silver Coulee beds of Wyoming and the known distribution of the species is restricted to that locality. McKenna (1960a) has assigned a fragmentary m1 from the Eocene Four Mile fauna of Colorado, and Gazin (1956a) a p4 from Bison Basin, Wyoming to Ectypodus cf. E. hazeni.

The specimens of N. hazeni from the type locality, Princeton Quarry, fall within, or very slightly beyond, the upper extreme of variation of the much larger sample of

Neoplagiaulax, cf. N. hazeni from Roche Percee in both dimensions and cusp formulae. Hopefully, further collecting from levels stratigraphically proximate to Princeton Quarry may permit a more accurate comparison between the two fossil populations. Qualitatively, with the exception of P4, comparable teeth in the two samples are nearly identical. Only two specimens of P4, PU 14432 and PU 14340, are known from Princeton Quarry. The last three or four cusps of PU 14432 are broken away but the recency of breakage is unknown (the tooth is shown complete in Jepsen's (1940) pl. IV, fig. 3, 3a). Jepsen (p.306) stated that "the last cusp is the highest" on P4. On PU 14340, however, the ultimate and penultimate cusps appear to be subequal in stature (see Fig. 7H-J). The summits of the crowns of P4's from Roche Percee, by contrast, are occupied by the penultimate (occasionally), antepenultimate (usually), or the fourth from last (occasionally) cusp. Further, the P4's from Roche Percee have a more convex and less steeply inclined anterior slope, more concave posterior slope, and the sides of the crown, at mid-length, are indented, rather than parallel. Apart from the cited differences between P4's of the two samples, the specimens from Roche Percee could, with little question, be lumped with N. hazeni.

Neoplagiaulax hunteri (Simpson, 1936)

(Figure 8; Tables 11-13)

Referred specimens.- p4: MMMN 447, UA nos. 9757, 9917, 9924, 9950, 9951, 9955, 9982, 9983, 10051, 10052, 10116, 10707, 10759, 11421, 11422, 11520, 11527, 11528, 11640; m1: MMMN 469, UA nos. 9749, 9787, 10114, 10314, 10680, 11440, 11442; m2: UA nos. 9952, 11475, 11477; P1: UA nos. 9851, 10010, 10373, 10418, 10457, 10458, 10496, 10536, 10540, 11665; P2: UA nos. 9849, 9944, 10430, 10463, 10528, 10780, 11666, 11673; P4: UA nos. 9823, 9913, 9945, 9957, 9977, 9997, 10001, 10006, 10007, 10133, 10137, 10196, 10254, 10300, 10403, 10611, 10954, 10955, 11457, 11458, 11529-11532; M1: UA nos. 10206, 10614, 11533; M2: UA nos. 9821, 10213, 10296, 10316, 10725, 11482.

Sites.- UAR2, UAR2a, UAR2d, and UAR2g, Ravenscrag Formation, Saskatchewan.

Known distribution.- Roche Percee local fauna, Ravenscrag Formation, Saskatchewan; Scarritt Quarry, Melville Member, Fort Union Formation, Montana (Simpson, 1936); Circle local fauna, Tongue River Formation, Montana (Sloan, in D.E. Russell, 1967); and Police Point locality, Ravenscrag Formation, Alberta (Krishtalka, 1973).

DESCRIPTION

p4.- In lingual view, the crown, which bears 15

Figure 8. Neoplagiaulax hunteri, Roche Percee local fauna, Saskatchewan: (A) labial, and (B) lingual view, UA 9955, left p4, length 4.9, about x8; (C) occlusal view, stereophotographic pair, composite left lower dentition, UA 9787 (m1 - length 2.8), UA 11477 (m2 - length 1.5), about x9; (D) occlusal view, stereophotographic pair, composite left upper dentition, UA 10418 (P1 - length 1.6), UA 11673 (P2 - length 1.4), about x10; (E) occlusal (stereophotographic pair), (F) labial, and (G) lingual view, UA 10196, left P4, length 3.5, about x8; (H) occlusal view, stereophotographic pair, UA 10614, right M1, length 3.3, about x8; (I) occlusal view, stereophotographic pair, UA 10725, left M2, length 1.5, about x8.

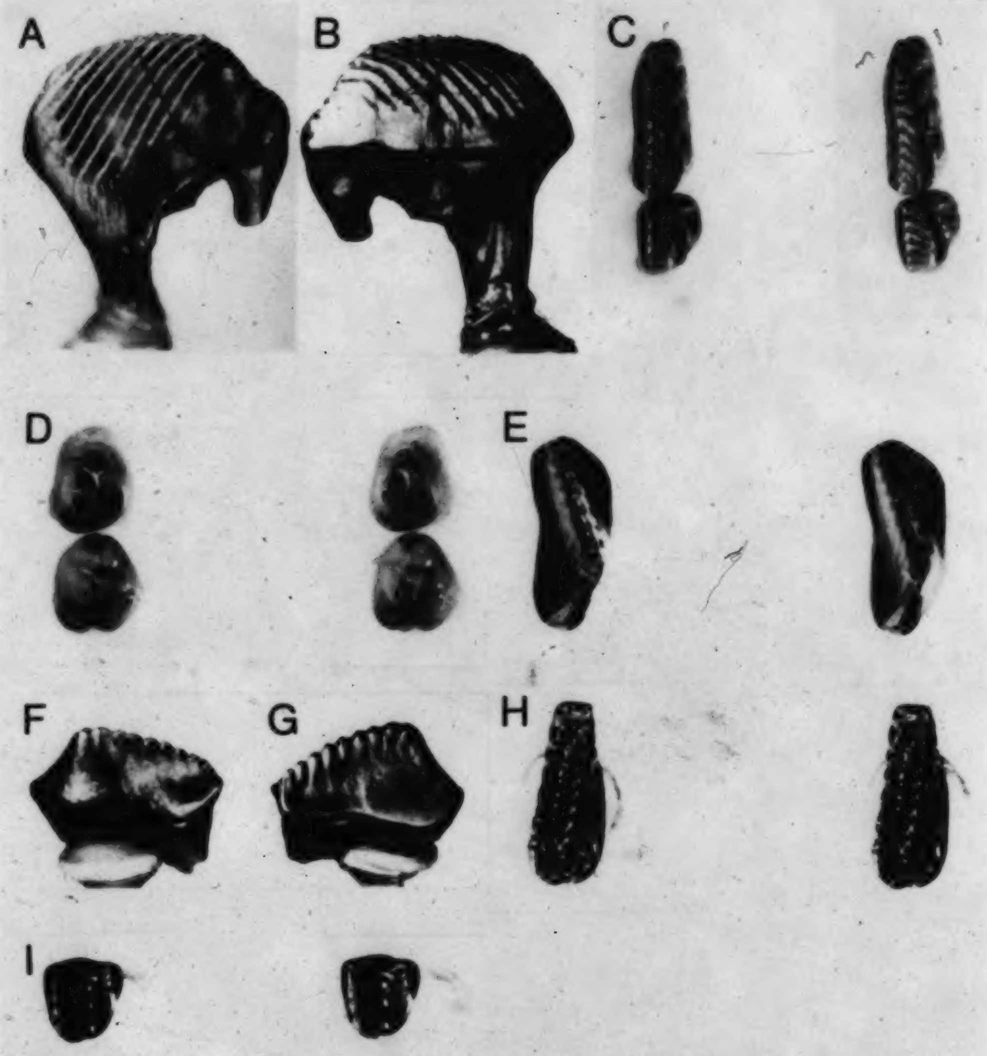
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Table 11. Measurements and descriptive statistics of the dentition of _Neoplagiaulax_ _hunteri_, Roche Percee local fauna, site UAR2a.

Measurement	N	OR	M±SE	SD	CV
p4 Length	2	4.6-4.9	4.75±.15	.21	4.5
m1 Length	5	2.5-2.8	2.66±.05	.11	4.3
Width	6	1.1-1.2	1.13±.02	.05	4.6
m2 Length	2	1.5	---	---	---
Width	2	1.2-1.3	1.25±.05	.07	5.6
P1 Length	7	1.5-1.8	1.61±.03	.09	5.6
Width	8	1.3-1.5	1.36±.03	.07	5.5
P2 Length	6	1.4-1.6	1.45±.03	.08	5.8
Width	6	1.2-1.5	1.30±.04	.11	8.4
P4 Length	6	3.4-3.6	3.52±.03	.08	2.1
Width	10	1.4-1.6	1.52±.02	.08	5.2
M1 Length	1	3.3	---	---	---
Width	1	1.4	---	---	---
M2 Length	5	1.5-1.6	1.56±.02	.05	3.5
Width	5	1.4-1.5	1.44±.02	.05	3.8

Table 12. Measurements and descriptive statistics of the dentition of Neoplagiaulax hunteri, Roche Percee local fauna, site UAR2.

Measurement	N	OR	M±SE	SD	CV
p4 Length	2	4.7-4.9	4.80±.10	.14	2.9
m2 Length	1	1.6	---	---	---
Width	1	1.3	---	---	---
P1 Length	1	1.7	---	---	---
Width	1	1.3	---	---	---
P2 Length	1	1.5	---	---	---
Width	1	1.4	---	---	---
P4 Length	7	3.1-3.5	3.33±.06	.15	4.5
Width	7	1.4-1.7	1.56±.04	.10	6.3

Table 13. Measurements and descriptive statistics of the dentition of *Neoplagiaulax hunteri*, Roche Percee local fauna, site UAR2g.

Measurement	N	OR	M±SE	SD	CV
P2 Length	1	1.5	---	---	---
Width	1	1.4	---	---	---

serrations (only four complete specimens were recovered) is nearly trapezoidal. The base and top of the crown are parallel to each other and the slightly convex anterior and straight posterior margins slope posterodorsal-anteroventrally and anterodorsal-posteroventrally, respectively. The distance between the bottom of the exodaenodont lobe and the dorsal margin of the crown is approximately four-fifths that of the anteroposterior length of the tooth. The height of the first serration above the anterobasal concavity is between one-third and one-half the anteroposterior length. The pattern of ridges descending from the first serration is variable but usually consists of a short labial ridge that converges with or joins the ridge from the second serration, a central ridge that bifurcates early after its origin and continues as two, indistinct ridges to near the anterobasal concavity (in UA 10707 an incipient serration and in UA 11520 a small swelling is developed at the point of bifurcation), and a lingual ridge of intermediate length that roughly parallels the other ridges of the lingual side. The area between the two bifurcating ridges is flat, sometimes grooved, and faces anterolingually. In about one-third of the specimens, the lingual ridge of the second serration is diverted posteriorly and joins the third ridge about half-way along its length. The anterobasal concavity is deep and squared dorsally.

One of the diagnostic features of the crown is that the labial side is decidedly convex in end view, rather than concave or flat as in most ptilodontoids; the lingual side is flat.

m1.- Cusp formula 11-12:4-5 (mode 11:4). The crown is anteroposteriorly elongate and overhangs the anterior, but not the posterior, root. Anteriorly, the cusps of the external row are pyramidal but become subcrescentic by mid-length and crescentic posteriorly. All of the external cusps are four-sided but increase in size and height from anterior to posterior to about the sixth cusp, from which point on they are relatively uniform. On most of the specimens a single vertical groove is present labially on each of the cusps of the external row, but wear, at least anteriorly, tends to make this a highly variable feature. The cusps of the internal row are taller and larger, and are flat and irregularly grooved on the valley-facing slopes and rounded lingually. The last three cusps are subequal in height and are taller and larger than the one or two anterior cusps.

m2.- All three referred m2's have a cusp formula of 6:2 and, in occlusal view, resemble a right-angled triangle although the hypotenuse, comprised of the lingual and posterior margins, is convex. The cusps of the external row are uniform in size, height, and shape, being broad, short, and crescentic. Those of the internal row are much more massive, the first being crescentic and taller than the second, which is triangular in cross section, tapering posteriorly. A third cusp can be incipiently developed on the posterior slope of the second.

P1.- The P1's referred here are similar to those of Type E, which are tentatively assigned to Neoplagiaulax, cf. N. hazeni (see below). Upper first premolars of N. hunteri, however, are more nearly triangular in occlusal outline, the posterior margin is flat rather than bluntly peaked as in Type E, the posterointernal cusp is usually directly opposite the posteroexternal cusp rather than also being slightly behind it, the cusps are more closely crowded together, and the enamel tends to be wrinkled.

P2.- The P2's of N. hunteri are structurally like those questionably referred to Neoplagiaulax, cf. N. hazeni (Type F) but differ in the following respects: slightly smaller, ridge connecting labial cusp and anterolingual cusps weak or absent, posterior face more steeply inclined and with tendency for more wrinkling of the coronal enamel.

P3.- No P3's definitely referable to N. hunteri were found although it is possible that they were mistaken for P3's tentatively referred to Neoplagiaulax, cf. N. hazeni (Type G). It appears, however, that P3's of N. hunteri do not possess a posterior expansion of the crown as is preserved on the posterior fragment of P3 (PU 14432) of N. hazeni and those placed in Type G.

P4.- Cusp formula 0-1:8-9:0 (mode 0:9:0). The single cusp of the external row, when present, is large and conical and situated dorsal and opposite to the second, third, or fourth cusp of the middle row. Subequal in size, the cusps of the middle row progressively increase in height posteriorly to the penultimate or ultimate cusp. Although wear is heaviest at the peak of the crown, the anterior slope on unworn or slightly worn specimens is slightly convex in side view; the posterior slope varies from almost straight to markedly concave. One specimen, UA 10254, is worn down to the pulp cavity such that a broad, flat facet is produced parallel to the base of the crown.

M1.- Cusp formula 8:12:7 (only one complete specimen). The cusps of the internal row originate opposite the fourth cusp of the middle row and progressively increase in size and height posteriorly. Those of the middle row are four-sided, crescentic, uniform in height, grooved on both sides, and increase in bulk from anterior to posterior. The external cusps are also uniform in height and increase in size from anterior to posterior; they are convex labially but medially are flat and marked by several irregular grooves. The presence of prominent grooves on the valley-facing slopes of the cusps is a diagnostic characteristic distinguishing M1's of _N_. _hunteri_ and _Neoplagiaulax_, cf. _N_. _hazeni_ from Roche Percee.

M2.- Cusp formula 1:4:4-5 (mode 1:4:4). The general coronal structure of the referred M2's is typical of most ptilodontoids; the internal row consists of crescentic cusps decreasing in size and height from anterior to posterior, the middle row of larger and more crescentic cusps, the first of which can be confluent with the second, and the external row is comprised of a single low cusp placed anteroexternally on the crown. A prominent ridge extends across the apex of the anteroexternal cusp and posterointernally to the base of the ultimate cusp of the middle row.

DISCUSSION

In size, serration count, and certain qualitative features of the crown (*e.g.* the trapezoidal lingual profile and convex labial side) the p4's referred above are very close to those of *N. hunteri* from Scarritt Quarry. AMNH 33869, an isolated P4, closely resembles the specimens from Roche Percee in its cusp formula, concave posterior slope, convex anterior slope, and high crown.[1] The Scarritt Quarry P4's, however, are, on the average, slightly shorter, the difference between the two samples approaching significance ($0.01<\text{Prob.}<0.05$) in this measurement.

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[1] The extreme height of the crown, especially, is not well illustrated in Simpson's (1936) fig. 2 of AMNH 33869. Simpson, in fact, noted that the P4's of *N. hunteri* most closely resembled those of *Ectypodus musculus* Matthew and Granger (1921) (see Granger and Simpson, 1929, fig. 35), which are very high crowned.

The m1's from Roche Percee consistently have more cusps in the external row than those from Scarritt Quarry (11 or 12 as opposed to 8 or ?9 (Simpson, 1937b)), but the m1's from Scarritt Quarry are generally poorly preserved and covered with shellac, thereby making observation of the miniscule anterior cusps extremely difficult if not impossible. USNM 33996 is perhaps the best preserved and, on this tooth, I obtained a cusp formula of 10:4.

AMNH 33890 and AMNH 35213, M1's from Scarritt Quarry, are similar to UA 10614 but have a more complete internal row, that is, it extends cranially to near the anterior margin of the tooth, whereas in UA 10614, which exhibits very little wear, the row originates opposite the fourth cusp of the middle row.

From the close and diagnostic similarities between fourth premolars in the samples from Roche Percee and Scarritt Quarry, it is inferred that the animals represented were probably conspecific. In its generally slightly larger size and higher cusp formula on m1, _N. hunteri_ from Roche Percee appears to be further advanced than the Scarritt Quarry _N. hunteri_ and tends towards the conditions seen in a later, larger, more cuspidate species of _Neoplagiaulax_ to be described by Sloan (pers. comm., 1975).

Genus *Mesodma*

Mesodma sp. P

(Figure 9; Tables 14,15)

Referred specimens.- Jaw fragment containing p4,m1: UA 10796; p4: UA nos. 9752, 9754, 9755, 9767, 9782, 9789, 10111, 10148, 10163, 10224, 10233, 10245, 10334, 10718, 10743, 10791, 10794, 10798, 10930, 11433-11435, 11522, 11523, 11629-11632, 11634; m1: UA nos. 9852, 10229, 10258, 10268, 10949, 11448, 11449; m2: UA nos. 10802, 11002; P4: UA nos. 10151, 10252, 10291, 10770, 10972, 10973; M1: UA nos. 10420, 10988, 10993, 11519; M2: UA nos. 10790, 11005.

Sites.- UAR2a and UAR2g, Ravenscrag Formation, Saskatchewan.

Known distribution.- Roche Percee local fauna, Ravenscrag Formation, Saskatchewan; Gidley Quarry, Lebo Member, Fort Union Formation, Montana (Sloan, pers. comm. to Krishtalka, 1973); Shotgun local fauna, Shotgun Member, Fort Union Formation, Wyoming (Sloan, pers. comm. to Krishtalka *et al*., 1975); Badwater Creek locality, Shotgun Member, Fort Union Formation, Wyoming (Krishtalka *et al*., 1975); Police Point locality, Ravenscrag Formation, Alberta (Krishtalka, 1973); and, questionably, from locality 40147, Black Peaks Formation, Texas (Schiebout, 1974).

Figure 9. *Mesodma* sp. P, Roche Percee local fauna, Saskatchewan: (A) labial, and (B) lingual view, UA 11522, left p4, length 2.5, about x10; (C) occlusal view, stereophotographic pair, composite left lower dentition, UA 10258 (m1 - length 1.6), UA 10802 (m2 - length 1.0), about x11; (D) labial, (E) lingual, and (F) occlusal view, stereophotographic pair, UA 10151, right P4, length 2.1, about x10; (G) occlusal view, stereophotographic pair, composite left upper dentition, UA 10420 (M1 - length 2.0), UA 11005 (M2 - length 1.0), about x10.

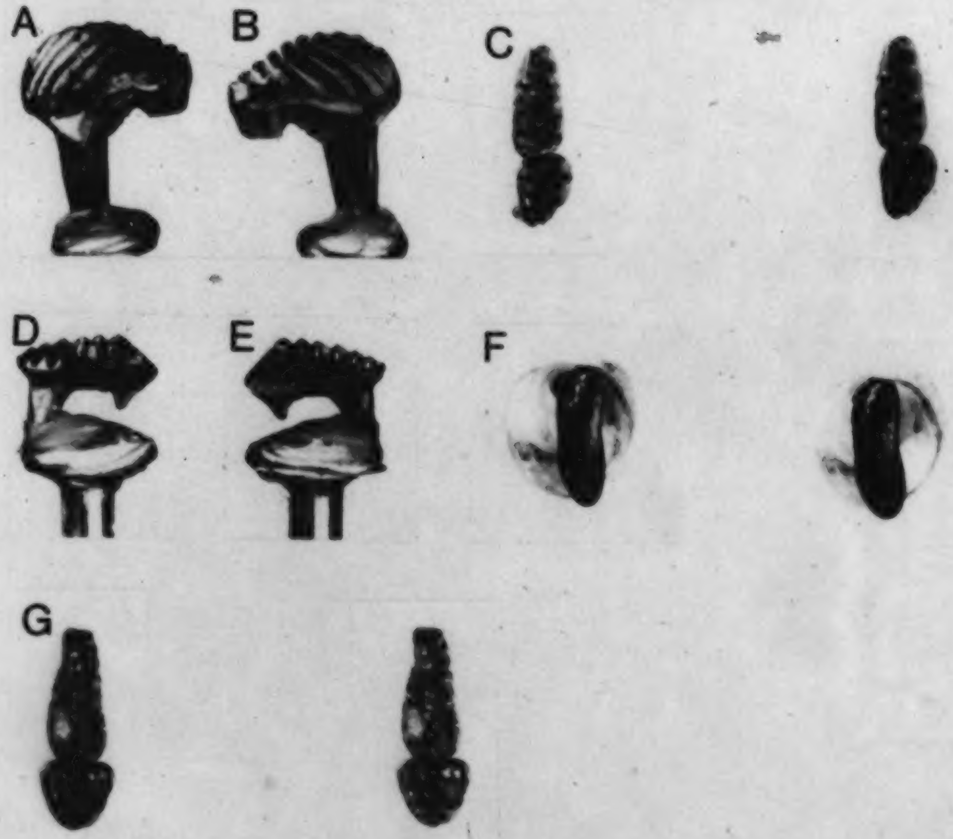
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Table 14. Measurements and descriptive statistics of the dentition of Mesodma sp. P, Roche Percee local fauna, site UAR2a.

Measurement	N	OR	M±SE	SD	CV
p4 Length	11	2.4-2.8	2.61±.03	.11	4.4
m1 Length	7	1.6-1.8	1.70±.03	.08	4.8
Width	7	0.7-0.8	0.76±.02	.05	7.1
m2 Length	1	1.0	---	---	---
Width	1	0.8	---	---	---
P4 Length	4	1.8-2.1	2.00±.07	.14	7.1
Width	4	0.6-0.7	0.68±.03	.05	7.4
M1 Length	4	2.0-2.2	2.10±.04	.08	3.9
Width	3	0.9-1.0	0.93±.03	.06	6.2
M2 Length	1	1.0	---	---	---
Width	1	1.1	---	---	---

Table 15. Measurements and descriptive statistics of the dentition of Mesodma sp. P, Roche Percee local fauna, site UAR2g.

Measurement	N	OR	M±SE	SD	CV
p4 Length	4	2.5-2.8	2.62±.08	.15	5.7
m1 Length	1	1.7	---	---	---
Width	1	0.8	---	---	---
Length p4/Length m1	1	1.65	---	---	---
m2 Length	1	1.0	---	---	---
Width	1	0.8	---	---	---
P4 Length	2	2.0	---	---	---
Width	2	0.7-0.8	0.75±.05	.07	9.4
M2 Length	1	1.0	---	---	---
Width	1	1.1	---	---	---

DESCRIPTION

p4.- The p4's referred to _Mesodma_ sp. P have nine (one specimen), 10 (12 specimens), or 11 (one specimen) serrations. In profile view the relatively low crown is taller anteriorly than posteriorly. The posterior slope is gentle and straight, commencing from the third or fourth serration, which is highest above the base line for measurement of the anteroposterior length. The enamel overlying the exodaenodont lobe is peaked ventrally. The height of the first serration above the anterobasal concavity is approximately one-third the length of the crown. Three short ridges, one anterolabially and two anterolingually, descend from the first serration. The most lingual of the three is variable in length and position but is usually very short and terminates by abutting the ridge descending from the second serration. All of the serrations, except the last two, bear well-defined arcuate ridges that extend anteroventrally down the labial and lingual sides of the crown and become progressively more widely separated posteriorly. Irregular wrinkling of the enamel occurs labial and ventral to the ultimate and penultimate serrations on unworn specimens. The anterobasal concavity is notched for the reception of p3.

m1.- Cusp formula 7:4. The m1's of _Mesodma_ sp. P from Roche Percee differ only slightly from the single referred specimen (UA 5752) from the Police Point locality

(Krishtalka, 1973) in that, in the latter, one fewer cusp is present in the external row and the two rows of cusps are more nearly parallel. The m1's from the Badwater Creek locality (Krishtalka *et al*., 1975) are larger than those referred here and are referable to *Microcosmodon conus* Jepsen, 1930b (see below).

m2.- Each of the two referred m2's has a cusp formula of 4:2 although the last two cusps of the external row are closely joined and separated only by a vertical groove medially. The groove is indistinct on most of the m2's of *Mesodma* sp. P from the Police Point locality (Krishtalka, 1973), which have a cusp formula of 3:2, but on at least two of the specimens (UA 5753 and UA 5754) the groove is incipiently developed. The m2 from Gidley Quarry (AMNH 35298) also has a cusp formula of 3:2.

P4.- The cusp formula of 3:5-7:0 (mode 3:6:0) for the P4's from Roche Percee is closely comparable to that listed for P4's of *Mesodma* sp. P by Krishtalka (1973) of 2-3:6-7 (one of his specimens (UA 5758) clearly has only five cusps in the middle row, therefore yielding the formula 2-3:5-7:0 (mode 3:6:0, personal observation)) and by Krishtalka *et al*. (1975) of 3:6.

UA 10972, a P4 from Roche Percee, has a small cusp developed posterior and dorsal to the tallest cusp of the middle row; however, this is regarded as an individual variant since similarly placed cuspules are incipiently developed and barely discernible on two other specimens (UA 10291 and UA 10973). In the latter two specimens and all other referred P4's, the ultimate cusp of the middle row is the tallest on the crown, one of the conditions usually considered diagnostic of _Mesodma_ (Sloan, pers. comm. to Krishtalka (1973)). Krishtalka (1973) has adequately described other features of the crown.

M1.- Cusp formula 7-8:9-10:4-5. The structure of the crown of M1 of _Mesodma_ sp. P has been described by Krishtalka (1973) and the specimens referred here do not differ appreciably. The specimen from the Badwater Creek locality (Krishtalka _et al_., 1975) is slightly larger.

M2.- The M2's of _Mesodma_ sp. P have a cusp formula of 1:3:3 and fall within the range of variation of the same species from the Police Point locality as outlined by Krishtalka (1973). The only qualitative difference worthy of note is that the first cusp of the middle row tends to be lower and more closely joined to the second cusp in the specimens from Roche Percee.

DISCUSSION

The specimens described above clearly fit the revised generic diagnosis of _Mesodma_ formulated by Clemens (1964) (see also Krishtalka (1973) and Krishtalka _et al_. (1975) for diagnostic characters of P4). The teeth of _Mesodma_ from Roche Percee are almost identical to those of _Mesodma_ sp. P from Gidley Quarry, the proposed type locality (Sloan, pers. comm. to Krishtalka, 1973) and especially to those from the Police Point locality (Krishtalka, 1973). The few slight differences, outlined above, are not considered to be taxonomically significant.

Mesodma sp. P is smaller than all other known species of *Mesodma* except *M. hensleighi* Lillegraven (1969) with which it is broadly comparable in size and very similar in structure. Teeth of *M. hensleighi* from the upper part of the Edmonton Formation, Alberta (UA collections), however, differ in the following respects: p4 slightly lower, distance between first serration and anterobasal concavity less, P4 with well developed posterobasal cuspule and with only one cusp in external row rather than three or four, and length:width ratio of P4 relatively low.

Lillegraven (1969, p.19) found "only meager evidence for consistent morphological differences" between *M. hensleighi* and *M. formosa* (Marsh, 1889). Specimens of *M. formosa*, *s.s.*, although slightly larger, are therefore also very similar to *Mesodma* sp. P. In fact, the cusp formula of 2:6:0 for the P4 of *M. formosa* given by Lillegraven (1969) and the tendency for four cusps to be developed in the external row of m2 are features closer to *Mesodma* sp. P than exhibited by *M. hensleighi*. Clemens (1964) gave a cusp formula for the P4 of *M. formosa* of 1-4:5-7:0-1 but, at that time, had not recognized the taxon later identified as *M.*

hensleighi in the samples from the Lance Formation. Whether subsequent recognition (Clemens, 1973) affected this formula was not stated although measurements of the p4's of both species were given. In any case, *Mesodma* sp. P appears to have descended from an ancestor such as *M. formosa* or *M. hensleighi*. The latest known occurrence of *M. formosa* is in the Purgatory Hill local fauna of Montana (Van Valen and Sloan, 1965), whereas *M. hensleighi* has been recognized only at Lancian horizons (Lillegraven, 1969; Clemens, 1973). Following a detailed analysis of intrageneric variation in *Mesodma*, Novacek and Clemens (in press) concluded that the Paleocene species of *Mesodma* were likely derived from *M. formosa* or *M. thompsoni* Clemens, 1964.

Genus *Mimetodon*

Mimetodon silberlingi (Simpson, 1935a)

(Figure 10A-G; Tables 16-18)

Referred specimens.- p4: UA nos. 9747, 9756, 9759, 9761, 9764, 9772, 9776, 9778, 9781, 9786, 9793, 9797, 9824, 10030, 10032-10035, 10047, 10056, 10057, 10104, 10129, 10132, 10149, 10159, 10160, 10177, 10183, 10193, 10201, 10222, 10240, 10299, 10312, 10313, 10324, 10333, 10335, 10360, 10411, 10498, 10509, 10515, 10525, 10585, 10591, 10609, 10616, 10620, 10623, 10646, 10648, 10658, 10667, 10698, 10700, 10712, 10715, 10724, 10744, 10757, 10760,

Figure 10. _Mimetodon_ _silberlingi_, Roche Percee local fauna, Saskatchewan: (A) labial, and (B) lingual view, UA 10788, right p4, length 3.1, about x10; (C) occlusal view, stereophotographic pair, composite left lower dentition, UA 10339 (m1 - length 2.1), UA 10162 (m2 - length 1.2), about x10; (D) labial, (E) lingual, and (F) occlusal view, stereophotographic pair, UA 10168, right P4, length 2.3, about x10; (G) occlusal view, stereophotographic pair, composite right upper dentition, UA 10126 (P4 - length 2.4), UA 10066 (M1 - length 2.9), UA 10150 (M2 length 1.4), about x10. _Mimetodon_ _silberlingi_?, Roche Percee local fauna, Saskatchewan: (H) labial, (I) lingual, and (J) occlusal view, stereophotographic pair, UA 10069, left P4, length 2.4, about x10.

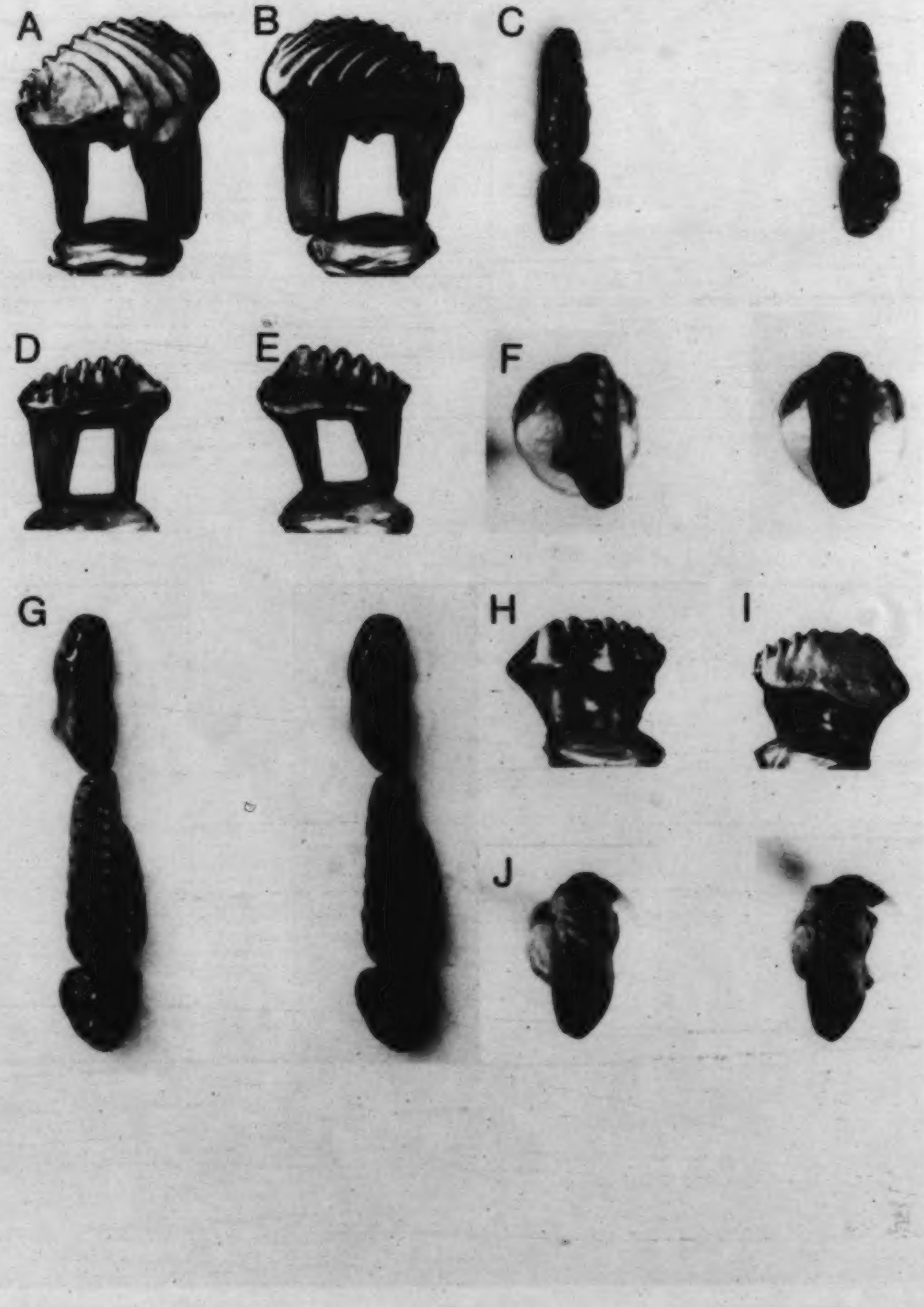
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Table 16. Measurements and descriptive statistics of the dentition of *Mimetodon silberlingi*, Roche Percee local fauna, site UAR2a.

Measurement	N	OR	M±SE	SD	CV
p4 Length	28	3.0-3.6	3.27±.03	.15	4.6
m1 Length	28	2.0-2.4	2.22±.02	.10	4.6
Width	31	0.8-1.1	0.94±.01	.07	7.1
m2 Length	11	1.2-1.4	1.31±.02	.07	5.4
Width	11	1.0-1.1	1.07±.01	.05	4.4
P4 Length	26	2.1-2.6	2.35±.02	.12	5.3
Width	25	0.7-1.0	0.83±.01	.07	9.0
M1 Length	39	2.3-3.0	2.75±.03	.19	6.8
Width	55	1.0-1.3	1.18±.01	.07	6.3
M2 Length	15	1.1-1.4	1.22±.02	.09	7.1
Width	15	1.1-1.3	1.25±.02	.06	5.1

Table 17. Measurements and descriptive statistics of the dentition of Mimetodon silberlingi, Roche Percee local fauna, site UAR2.

Measurement	N	OR	M±SE	SD	CV
p4 Length	2	3.1-3.2	3.15±.05	.07	2.2
m2 Length	1	1.4	---	---	---
Width	1	1.3	---	---	---
M1 Length	2	2.9	---	---	---
Width	4	1.1-1.2	1.15±.03	.06	5.0

Table 18. Measurements and descriptive statistics of the dentition of _Mimetodon_ _silberlingi_, Roche Percee local fauna, site UAR2g.

Measurement	N	OR	M±SE	SD	CV
p4 Length	1	3.1	---	---	---
m1 Length	1	2.2	---	---	---
Width	1	0.9	---	---	---
m2 Length	1	1.2	---	---	---
Width	1	1.1	---	---	---
P4 Length	3	2.3-2.5	2.40±.06	.10	4.2
Width	2	0.8-0.9	0.85±.05	.07	8.3
M1 Length	4	2.6-2.8	2.65±.05	.10	3.8
Width	4	1.1-1.2	1.15±.03	.06	5.0

10786, 10788, 10801, 10951-10953, 11428, 11429, 11431, 11432, 11436, 11604-11624, 11635, 11702; m1: UA nos. 9770, 9785, 10084, 10152, 10169, 10242, 10244, 10251, 10267, 10288, 10297, 10302, 10321, 10339, 10350, 10406, 10533, 10686, 10742, 10795, 10800, 10936-10948, 10950, 11437-11439, 11526, 11625-11627; Jaw fragment with m1,m2: UA 10000; m2: MMMN 414, UA nos. 10044, 10049, 10097, 10162, 10191, 10197, 10355, 10664, 10764, 10997-10999, 11001, 11476, 11478; P4: UA nos. 9836, 9842, 9994, 10092, 10126, 10130, 10134, 10147, 10168, 10170, 10204, 10228, 10264, 10287, 10374, 10379, 10413, 10527, 10656, 10673, 10779, 10799, 10881, 10895, 10964, 10966-10971, 11459-11465, 11628, 11633; M1: MMMN nos. 417, 561, UA nos. 9766, 9780, 9790, 10045, 10048, 10055, 10066, 10070, 10074, 10077, 10109, 10113, 10153, 10208, 10212, 10216, 10217, 10226, 10232, 10263, 10293-10295, 10306, 10343, 10344, 10366, 10387, 10394, 10412, 10577, 10578, 10594, 10603, 10605, 10615, 10630, 10654, 10689, 10717, 10745, 10772, 10777, 10778, 10787, 10864, 10887, 10974, 10975, 10978-10981, 10983, 10986, 10987, 10989, 10990, 10992, 11505-11517; M2: UA nos. 9806, 9840, 10150, 10166, 10178, 10200, 10351, 10365, 10368, 10423, 10696, 11003, 11004, 11497-11499, 11501, 11701.

Sites.- UAR2, UAR2a, and UAR2g, Ravenscrag Formation, Saskatchewan.

Known distribution.- Roche Percee local fauna, Ravenscrag Formation, Saskatchewan; Rock Bench Quarry, Polecat Bench Formation, Wyoming (Jepsen, 1940); Gidley Quarry, Lebo Member, Fort Union Formation, Montana (Simpson, 1935a, 1937a); Olive local fauna, Tongue River Formation, Montana (Sloan, in D.E. Russell, 1967); Police Point locality, Ravenscrag Formation, Alberta (Krishtalka, 1973); localities 40147 and 41365, Black Peaks Formation, Texas (Schiebout, 1974); and, questionably, from the Shotgun local fauna, Shotgun Member, Fort Union Formation, Wyoming (Sloan, in D.E. Russell, 1967).

DESCRIPTION

The dentition of Mimetodon silberlingi has never been adequately described and therefore will be treated in detail here.

p4.- Ten (16 specimens), 11 (13 specimens), or 12 (four specimens) serrations may be present on p4. Two short ridges, situated anterolabially and anterolingually, descend from the first serration and are separated by a central ridge that bifurcates a short distance ventral to its origin. At the point of bifurcation a small swelling (three specimens) or serration (seven specimens) can be present. During the initial analysis it was thought that those p4's having this relatively low 'first' serration represented a separate phenon, but they are now believed to represent only individual variants, especially since intermediates do occur and no other structural differences were found. The height of the true first serration above the anterobasal concavity is slightly greater than one-third the length of the crown.

In labial view the crown is relatively low, front higher than rear, and the third or fourth serration is highest above the base line for measurement of the anteroposterior length. The exodaenodont lobe, although variably developed, is quite peaked ventrally, having an obliquely straight anterior margin and a relatively vertical, and again, straight, posterior margin. Vertically oriented, irregular ridges descend both labially and, to a lesser extent, lingually from the last two or three serrations.

m1.- Cusp formula 8-11:4-5 (mode 9:4). The first four or five cusps of the external row are four-sided and pyramidal and increase in size and height posteriorly. The remaining cusps in this row are subcrescentic to crescentic but are all subequal in height; the terminal cusp is longer than those anterior to it. When five cusps are present in the internal row, the first cusp is merely a small cone; when only four cusps occur, the first cusp is much larger and set well back from the anterior margin of the crown. The four main cusps of the internal row are much taller than those externally and are subequal in height (except for the first, which is usually shorter in unworn specimens), but increase in bulk from anterior to posterior. They are rounded lingually and flattened on their valley-facing slopes. The ultimate cusp in this row is very long and could be considered to be two cusps. An anomalous row of six tiny cuspules is developed ventral and labial to the sixth to ninth cusps of the external row on UA 10938.

Only one specimen, UA 10251, bears an accessory root but all of the referred m1's possess a low, interradicular crest between the quadrate or rectangular anterior root and the anteroposteriorly compressed posterior root.

m2.- Cusp formula 5:2, but in at least four specimens the fourth and fifth cusps of the external row are so closely joined that only a single cusp appears to be present. The cusps of the external row are crescentic in cross section and subequal in size and height, except the ultimate cusp, which is little more than an elongate, raised rim attached to the penultimate cusp. A short vertical groove is present medially on the first external cusp of most specimens, whereas a much longer groove invariably ascends the medial face of the ultimate cusp, bifurcating as it passes dorsally. The two internal cusps are much larger than those externally, the anterior one being taller, shorter (lengthwise), and more crescentic.

The two anteroposteriorly compressed roots can be joined at their bases for a short distance ventrally.

P4.- Cusp formula 2-5:6-8:0 (mode 3:6:0). Schiebout (1974, p.12) recently described two posterior fragments of

P4's of M. silberlingi from Tiffanian beds of Texas. These fragments "have a slightly concave posterior slope" and "the ultimate, penultimate, and antipenultimate (sic) cusps are very nearly the same height." The large sample recovered from Roche Percee permits delimitation of the variability in these and other attributes. The majority of P4's do have a slightly concave posterior slope whereas a few have a straight slope. The ultimate cusp is usually tallest on the crown but, in four specimens, the ultimate and penultimate are subequal in height and, in two, the last three cusps are of nearly equal height. Occasionally (in two specimens), one or two anomalous cuspules are developed along the posterior slope; the basal cuspule is usually developed to some degree. The anterior slope is invariably slightly convex.

The relative sizes and the positions of the external cusps vary greatly but, most commonly, three main cusps are developed lateral and slightly posterior to the first three cusps of the middle row. Smaller cusps or cuspules may be present anterior and/or posterior to the principal cusps.

A low interradicular crest and occasionally accessory roots are situated between the two primary roots.

M1.- Cusp formula 8-10:11-13:4-8 (mode 9:12:6). In profile aspect the crown is concave ventrally. The internal cusp row terminates lingual to the fourth, fifth, or sixth cusp, usually the fourth or fifth, of the middle row. The more central cusps of the internal row are larger and more crescentic than those either anteriorly or posteriorly. The first two or three cusps of the middle row are four-sided and pyramidal, the fourth and fifth are usually subcrescentic, and the remainder are crescentic in horizontal section. They progressively increase in size from anterior to posterior, as do those of the external row, which are flat medially and rounded labially.

The base of the anterior root is very long, occasionally extending for over one-half the length of the crown, and is laterally compressed. The posterior root, by contrast, is anteroposteriorly flattened. Accessory roots are commonly developed and, when present, can number up to four.

M2.- Cusp formula 1:3:3-4 (mode 1:3:3). The cusps of the internal row are crescentic and decrease in height from anterior to posterior. Those of the middle row are taller and even more crescentic. The first cusp in the row is the lowest.

The anterior root is very wide and anteroposteriorly compressed, whereas the posterior root, although of the same length, is smaller and round in cross section.

DISCUSSION

Jepsen (1940) erected the genus _Mimetodon_ to include _Mimetodon_ _churchilli_ Jepsen, 1940, _Ptilodus_ _trovessartianus_

(Cope, 1882a), and ?Ptilodus douglassi, a viewpoint that Sloan followed in 1966 (in Van Valen and Sloan, fig. 5). Sloan (pers. comm., 1975) currently believes that the latter two species should be allocated to Parectypodus and Neoplagiaulax, respectively. However, there is good reason to regard the douglassi form as a species of Ptilodus, and one that may, in fact, not be separable from Ptilodus montanus (see above). Further, Sloan, who in 1966 referred ?Ectypodus silberlingi to Mesodma, now would recognize it as the second species of Mimetodon (pers. comm. to Krishtalka (1973) and Schiebout (1974)).

Mimetodon silberlingi is a species widely distributed in space (Texas (Schiebout, 1974) to Alberta (Krishtalka, 1973)) and time (Torrejonian to Tiffanian). Except for the two fragmentary P4's that Schiebout (1974) described, the upper dentition was previously unknown. Although tentatively, specimens of upper teeth from the Roche Percee local fauna are assigned to M. silberlingi on the basis of size and frequency (and structure in the case of P4's). M. silberlingi, Neoplagiaulax, cf. N. hazeni, and Ptilodus kummae are by far the most common multituberculate species in the fauna and are quite disjunct in size, M. silberlingi being the smallest of the three. Relative to other teeth of M. silberlingi, m2's and M2's are about one-half as numerous. These teeth probably fell through the screening boxes, which had a mesh of 18 openings to the inch.

Slight differences are discernible between the Roche Percee *M. silberlingi* and USNM 9798, the type specimen, and AMNH 35499, both lower jaws from Gidley Quarry. For the present, these dissimilarities are interpreted as geographical and chronological variants of the same species. Lower fourth premolars of USNM 9798 and AMNH 35499 have a deeper anterobasal concavity for reception of p3, the exodaenodont lobe appears to be slightly smaller, and the ridges are parallel, rather than diverging slightly ventrally. Appreciable differences between the lower molars of USNM 9798, AMNH 35499 (only m1 preserved), and the Roche Percee specimens were not observed.

Fourth premolars of *Mesodma* sp. P and *Mimetodon silberlingi* are very difficult to distinguish in the Roche Percee local fauna and were initially dissociated by the drawing of camera lucida outlines to delimit the ranges of variation in both size and shape. Subsequent comparison of the two clusters showed that p4's of *Mesodma* sp. P are smaller than those of *Mimetodon silberlingi* and differ in the following qualitative attributes: very slightly lower first serration, posterior slope slightly more inclined, and last two or three serrations without vertically oriented, anteriorly convex wrinkles on the lingual side as in *Mimetodon silberlingi*. Upper fourth premolars of the two species overlap in size and are therefore even more difficult to distinguish. Upper fourth premolars of *Mesodma* are, however, generally lower and have a straight rather than slightly convex anterior slope, straight rather than usually concave posterior slope, and posterobasal cusps absent. These distinctions are nevertheless minor and consequently one or more of the smaller P4's here identified as *Mimetodon silberlingi* may in fact be correctly allocated to *Mesodma* sp. P and *vice versa*.

Mimetodon silberlingi?

(Figure 10H-J)

Referred specimen.- P4: UA 10069.

Site.- UAR2a, Ravenscrag Formation, Saskatchewan.

DESCRIPTION AND DISCUSSION

A single P4, measuring 2.4 by 1.1 mm and with a cusp formula of 4:7:0, is probably an extreme variant of *Mimetodon silberlingi*. It differs from other P4's of *M. silberlingi* principally in its taller crown, lower length:width ratio, the absence of a posterobasal cuspule, and its generally more massive construction.

Genus Ectypodus

Ectypodus, cf. E. powelli Jepsen, 1940

(Figure 11)

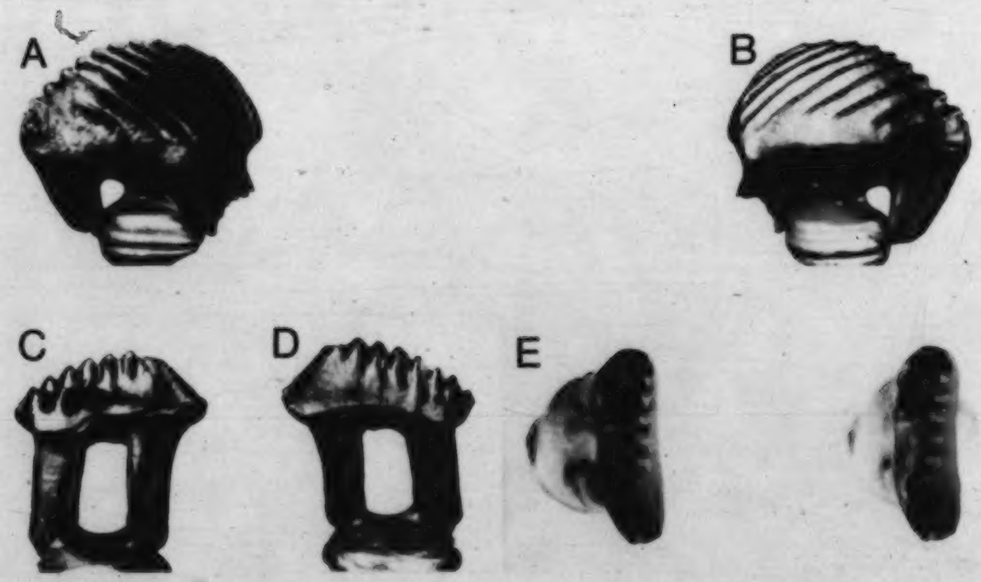
Referred specimens.- p4: UA nos. 10031, 10663, 11430, 11524, 11534-11536; P4: UA nos. 10210, 10340, 10965.

Sites.- UAR2a and UAR2g, Ravenscrag Formation, Saskatchewan.

DESCRIPTION

p4.- Each of the two complete p4's, UA 11430 (length 3.6 mm) and UA 11524 (length 3.5 mm), have 11 serrations. Relative to p4's of Mimetodon silberlingi and Mesodma sp. P, these p4's, in profile view, have a longer and more gentle anterior slope and the posterior portion of the blade is higher, thus giving the crown a more symmetrically arcuate appearance. The height of the first serration above the anterobasal concavity is about two-fifths the anteroposterior length of the crown. The ridges descending ventrolabially from the second serration on both the labial and lingual sides of the crown usually (in five of six specimens) merge faintly with those descending from the first serration. In UA 11524, however, the second lingual ridge turns to join the third, rather than the first, ridge. One of the most distinctive features is the prominent posterolabial shelf, which is much larger than in either Mimetodon silberlingi or Mesodma sp. P. Opposite to this

Figure 11. Ectypodus, cf. E. powelli, Roche Percee local fauna, Saskatchewan: (A) labial, and (B) lingual view, UA 11430, right p4, length 3.6, about x10; (C) labial, (D) lingual, and (E) occlusal view, stereophotographic pair, UA 10210, right P4, length 2.8, about x10.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landmark (that is, posterolingually on the tooth) a conical cuspule, projecting lingually, is developed on UA 11524. The enamel labial and ventral to the last two serrations, although worn by tooth-on-tooth contact, was crenulated. The exodaenodont lobe is not large and is peaked ventrally. A short interradicular crest is developed.

P4.- The only complete and unworn specimen referred here (UA 10210 - 2.8 by 1.1 mm) has the following features: cusp formula 3:7:0, straight posterior slope, slightly convex anterior slope, and terminal cusp tallest in the middle row (although the tip of this cusp is broken away, it appears to have been the tallest). In occlusal aspect the lingual margin of the crown is concave, the labial margin is indented at mid-length.

The three cusps of the external row increase in size posteriorly, the last one being opposite the third cusp of the middle row. The enamel at the base of the labial side of the crown is not straight as in _Mesodma_ sp. P but rather is deflected dorsally up the posterior root. A very small basal cuspule is developed at the bottom of the posterior slope of the crown.

The roots of UA 10210 are nearly equal in size and are relatively stout.

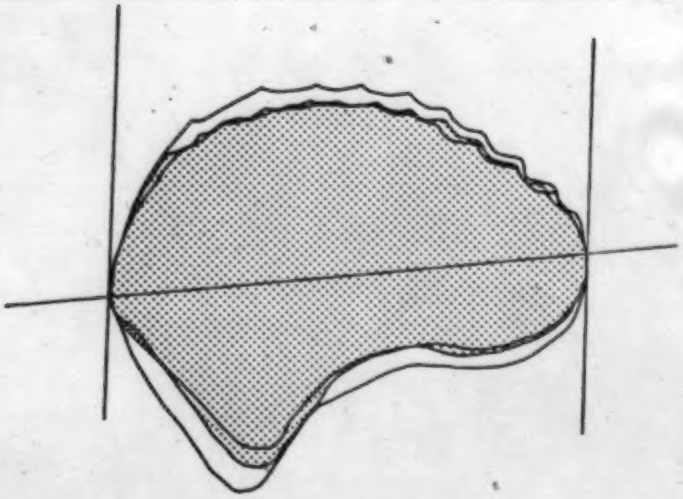
DISCUSSION

The association of the P4's with the p4's, both of which are infrequent in the sample and tend to be intermediate in size between *Mimetodon silberlingi* and *Neoplagiaulax hunteri*, of this taxon is tentative.

Isolated p4's of *Neoplagiaulax* and *Ectypodus* can be very difficult to distinguish but in *Ectypodus* the fourth serration, rather than the fifth, sixth, or seventh, is the highest on the crown, and the anterior slope is generally more convex than in *Neoplagiaulax* (Sloan, pers. comm., 1975). In these features the Roche Percee p4's probably should be referred to *Ectypodus*. This interpretation gains support when the P4's are taken into consideration. On UA 11430 and UA 11524 the terminal cusp is tallest in the middle row, both anterior and posterior slopes are almost straight, and the posterior basal cuspule is very weak, all diagnostic characteristics of *Ectypodus* (Sloan, pers. comm., 1975).

Of the known and described species of *Ectypodus*, the Roche Percee species is significantly larger than *E. tardus* (Jepsen, 1930a) and smaller than *E. musculus*. Lower fourth premolars of *E. powelli* are, however, only slightly smaller, are similar in serration count, and have a similarly small exodaenodont lobe but, when drawn to the same scale (Fig. 12), have a relatively higher crown and a greater distance between the anterobasal concavity and the first serration.

Figure 12. Diagrammatic outline, drawn with camera lucida, of labial profiles of p4's of *Ectypodus powelli* (PU 14425 - the only complete and relatively unworn p4 from Princeton Quarry, Wyoming - unstippled) and *Ectypodus*, cf. *E. powelli* (UA 11430 and UA 11524 - Roche Percee local fauna, Saskatchewan - stippled). Vertical straight lines mark the anterior and posterior margins; the nearly horizontal, straight line is drawn through the peak of the anterobasal concavity and along the top of the posteroexternal ledge.



The posterolabial shelf, or ledge, of p4's of _E_. _powelli_ is less well developed than on the UA specimens. These differences probably preclude a conspecific assignment; further collecting, both at Princeton Quarry levels and at Roche Percee may, however, provide evidence that will negate or enhance the differences between the two groups. Upper fourth premolars of _E_. _powelli_ are unknown. Besides the type locality at Princeton Quarry, _E_. _powelli_ is also known from Dell Creek Quarry, Hoback Formation, Wyoming (Dorr, 1952) and from the Olive and Circle local faunas, Tongue River Formation, Montana (Sloan, in D.E. Russell, 1967).

Suborder Taeniolabidoidea

Family Eucosmodontidae

Genus _Microcosmodon_

Microcosmodon _conus_ Jepsen, 1930b

(Figures 13,14; Tables 19,20)

Referred _specimens_.- Lower incisor: UA 11705; m1: UA nos. 10027, 10203; m2: UA nos. 10076, 10304; I2: UA nos. 11710-11714; M1: UA nos. 10083, 10143, 10976, 10982, 11518.

Sites.- UAR2 and UAR2a, Ravenscrag Formation, Saskatchewan.

Known _distribution_.- Roche Percee local fauna, Ravenscrag Formation, Saskatchewan; Princeton Quarry,

Figure 13. Microcosmodon conus, Roche Percee local fauna, Saskatchewan, stereophotographic pairs: (A) occlusal, and (B) dorsolabial view, UA 10027, right m1, length 2.4, about x11; (C) occlusal view, UA 10304, left m2, length 1.4, about x10; (D) occlusal view, UA 10976, left M1, length 2.5, about x11; (E) labial, and (F) lingual view, UA 11712, right I2, maximum diameter 1.9, about x10. Microcosmodon conus, Princeton Quarry, Wyoming: (G) occlusal view, stereophotographic pair, PU 14463, length 2.8, about x10.

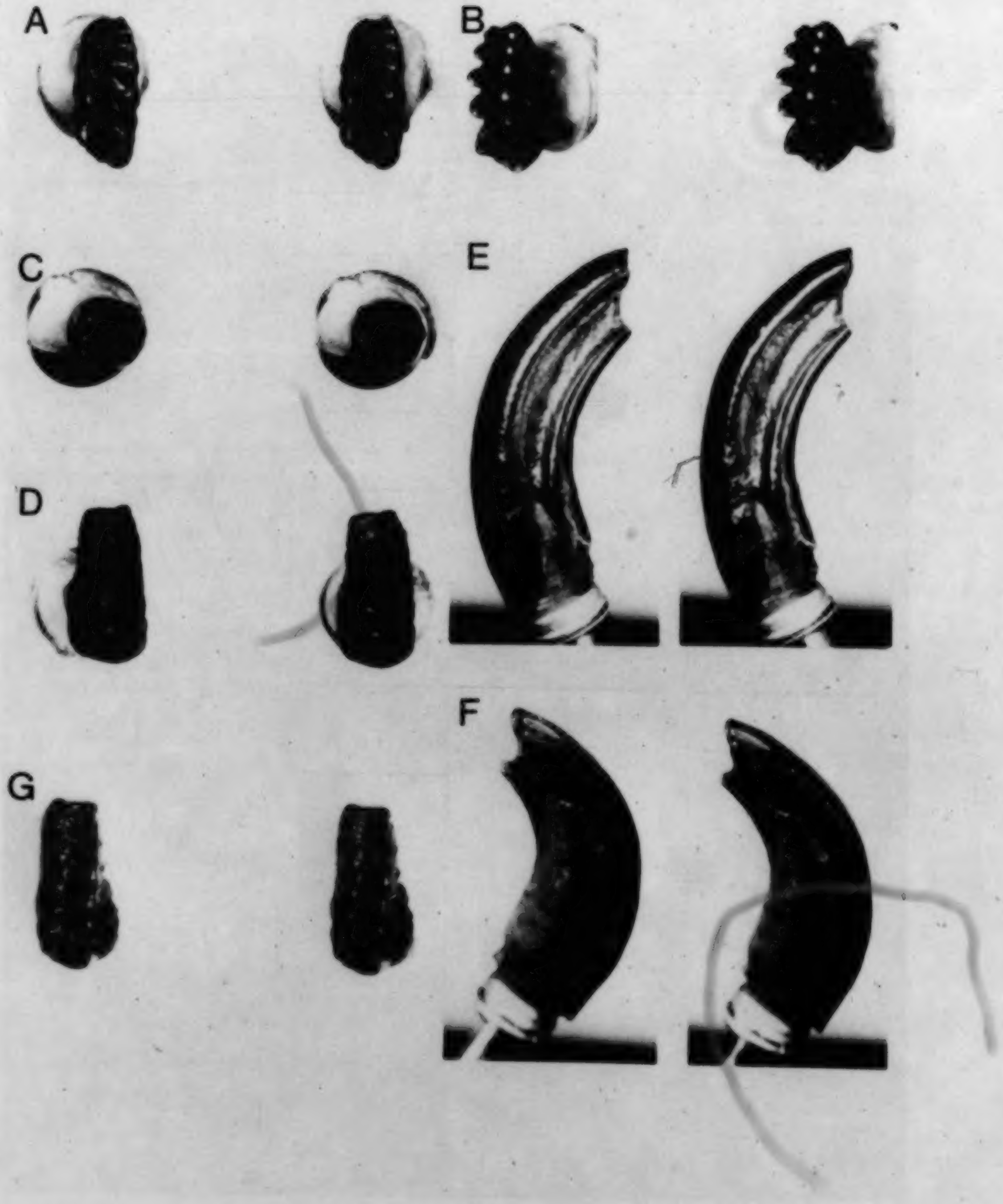

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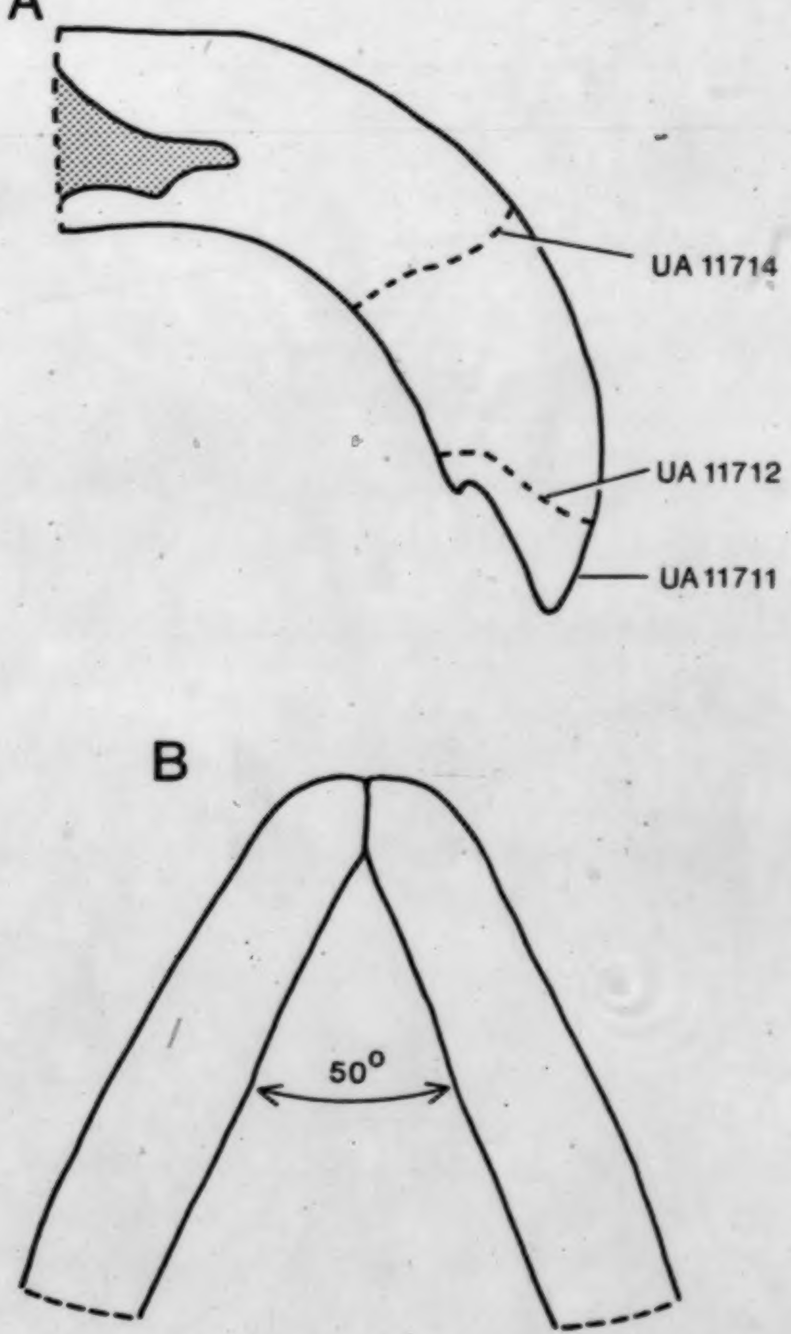
Figure 14. Microcosmodon conus, Roche Percee local fauna, Saskatchewan: (A) diagrammatic outline, drawn with camera lucida, of labial side of fragmentary I2's showing progressive stages of wear: UA 11711 - unworn, UA 11712 - moderately worn, UA 11714 - heavily worn. Stippled area indicates area not covered by enamel. (B) diagrammatic outline, drawn with camera lucida, of dorsal view of paired I2's showing amount of divergence towards the roots.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UA 11714
UA 11712
UA 11711
B
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Table 19. Measurements and descriptive statistics of the dentition of *Microcosmodon conus*, Roche Percee local fauna, site UAR2a.

Measurement	N	OR	M±SE	SD	CV
m1 Length	1	2.4	---	---	---
Width	1	1.1	---	---	---
m2 Length	2	1.4	---	---	---
Width	2	1.2-1.3	1.25±.05	.07	5.6
I2 Max. diameter	3	1.7-1.9	1.83±.07	.12	6.3
Min. diameter	3	1.1-1.2	1.17±.03	.06	4.9
M1 Length	5	2.5-2.7	2.58±.04	.08	3.2
Width	5	1.3	---	---	---

Table 20. Measurements and descriptive statistics of the dentition of *Microcosmodon conus*, Roche Percee local fauna, site UAR2.

Measurement	N	OR	M±SE	SD	CV
Lower incisor					
Max. diameter	1	2.1(est.)	---	---	---
Min. diameter	1	0.9(est.)	---	---	---
m1 Length	1	2.4	---	---	---
Width	1	1.1	---	---	---
I2 Max. diameter	1	1.8	---	---	---
Min. diameter	1	1.0	---	---	---

Polecat Bench Formation, Wyoming (Jepsen, 1930b); Schaff Quarry, Polecat Bench Formation, Wyoming (personal observation); Badwater Creek locality, Shotgun Member, Fort Union Formation, Wyoming (Krishtalka et al., 1975).

DESCRIPTION

Lower incisor.- Only a single, fragmentary, water-worn lower incisor (UA 11705) can be assigned to this species with any confidence; both the tip of the crown and the root are broken away. A raised rim marks the ventromedial margin of the transversely flattened and curved crown. Further details of the crown are marred by extensive abrasion of the tooth.

m1.- Cusp formula 9:5 (UA 10027) and 8:5 (UA 10203). UA 10027 is almost unworn and a distinct separation of the last cusp of the external row into two is evident. In both specimens, the cusps of the external row progressively decrease in height anteriorly and posteriorly from the fifth, which is also the most massive. Anteriorly, the cusps are subcrescentic but become strongly crescentic posteriorly. Almost parallel to one another, the two rows of cusps are separated by a highly irregular, labially convex furrow. The cusps of the internal row increase in size from anterior to posterior, but increase in height from both ends towards the third, thus reflecting the arched nature of the crowns. A prominent vertical groove marks the valley-facing slope of each cusp except the last, which bears two. The ultimate cusps of both rows are connected by a high, papillate ridge, which is sigmoidal and strongly angled anterointernal-posteroexternally.

Only the bases of the two, apparently subequal roots are preserved on UA 10027, but lingually, at mid-length, a small accessory root also supported the crown. UA 10203 does not possess accessory roots.

m2.- Although the cusp formula of the two complete m2's referred here is 4:2, the ultimate cusp of the external row is little more than a raised, posteriorly-extending rim attached to the penultimate cusp. The first three external cusps are crescentic in cross section and are subequal in height. Much larger, more widely separated, and more strongly inclined posteriorly than the cusps of the external row, the two internal cusps are both strongly crescentic and are grooved on their valley-facing slopes. As on m1, the posterior margin of the crown is not straight but sigmoidal. The two rows of cusps are subequal in height.

I2.- The second upper incisor is a long, curved bicuspid tooth that is completely covered by enamel labially. Lingually the enamel is presented as a narrow, dorsal strip, which follows the curve of the tooth and expands distally to cover the tip of the crown. The root of the tooth carries no enamel. A shallow longitudinal trough, which becomes shallower proximally, interrupts the elliptical cross section of the crown labially. Distally this trough divides the tooth into a large anterior cusp and a smaller posterodorsal cusp. Wear produces a broad facet that effaces the distinction between these two cusps.

M1.- Cusp formula 7:8:5?, 6?, or 7?. In lateral profile the crown is concave. The internal row of cusps terminates opposite the junction of the fourth and fifth cusps of the middle row and bears approximately five or six irregular and indistinct cuspules. Cusps of the external row, of which the fourth and fifth are the largest, are conical except for a medial flattening. The cusps of the middle row are four-sided and crescentic, especially posteriorly, and also progressively increase in size posteriorly.

From four to eight accessory roots, of varying sizes, augment the two stout and short primary roots in support of the crown. The anterior root is rectangular and laterally compressed, whereas the posterior root, extending dorsolingually, is anteroposteriorly flattened.

DISCUSSION

The lower incisor and the lower molars from Roche Percee have been compared with those of Microcosmodon conus from Princeton Quarry that Jepsen (1930b, 1940) described and with three undescribed specimens (PU 19366 (p4,m1); PU 19393 (p4,m1); and PU 19438 (lower incisor, p4)) from Schaff Quarry in the Polecat Bench Formation. Homologous teeth in these specimens are almost identical and are clearly referable to the same species. Second upper incisors from Roche Percee are very similar in size and structure to PU 14429, referred to either *M. conus* or *Pentacosmodon pronus* Jepsen, 1940. The occurrence of these unique I2's at Roche Percee with several other teeth of *M. conus* but with none of *P. pronus* strongly suggests that this kind of upper incisor belongs to the former species but, of course, no positive evidence exists to suggest that *P. pronus* did not have a similar I2.

The allocation of the M1's to *M. conus* is tentative inasmuch as they were not found in association with the lowers. However, this identification is supported, in addition to the size and frequency data, by the occurrence of similar, but slightly smaller, M1's with an undoubted p4 (CM 16123) of *M. conus*[1] at the Badwater Creek locality in Wyoming (see Krishtalka *et al*., 1975) and by a superficial resemblance to M1's of several other eucosmodontids (*e.g. Stygimys*, *Eucosmodon*, *etc*.) (curiously enough, there is also a very striking resemblance to M1's of the neoplagiaulacid *Cimexomys minor* Sloan and Van Valen, 1965).

PU 14463, an M1 that Jepsen (1940, p.309) questionably assigned to *Ectypodus powelli*, is identical to the M1's from

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[1] CM 16183, identified by Krishtalka *et al*. (1975) as a P4 of *Mesodma* sp. is, without question, a p4 of *Microcosmodon conus*.

Badwater Creek and Roche Percee referred to M. conus (see Fig. 13E) and is therefore placed in the latter species.

The m1's of M. conus have, characteristically, an arched profile of the crown and strongly crescentic cusps in the external row (especially posteriorly); the internal cusps, when little worn, are tall and recurved, and the crown is usually supported by one or more accessory roots. This combination of features is present in the Roche Percee specimens but not in those m1's that Krishtalka et al. (1975, see fig. 19; also note that the m1 figured is CM 16151, not CM 16149 as listed) assigned to M. conus; the latter m1's are also considerably smaller than m1's of M. conus from the Polecat Bench Formation (Jepsen, 1940). Instead, however, m1's that Krishtalka et al. (1975) referred to Mesodma sp. are unquestionably referable to M. conus (see fig. 14 in Krishtalka et al, 1975). Details of the crown of one of the specimens (CM 16188) are obscured by extensive wear but the crown is supported by three roots and is therefore questionably referred to M. conus with the other, more well preserved, specimens.

Three of the upper incisors of M. conus from the Roche Percee local fauna are preserved distally and are in different stages of wear (see Fig. 14A). A medial interdental wear facet (see Fig. 13G) is preserved on two of these teeth (the third is unworn) and indicates that the upper incisors converged distally from their alvecli at an internal angle of approximately 50° (Fig. 14B). The lower incisors, however, were almost parallel to one another. This relationship between upper and lower incisors readily explains the functional relationship between these teeth. The vertical axes of the upper and lower incisors met at an angle, the lower incisors being guided by and fitting into the terminal part of the longitudinal groove on the labial side of the upper incisors. As a result, the wear surface observed on the lower incisor of PU 19438 from Schaff Quarry, is transversely convex, rather than flat. The bicuspid nature of the terminal part of I2 was, early in ontogeny, obscured by wear but the longitudinal groove still served to guide the lower incisor into proper occlusion. Little wear was required before the pulp cavities on the upper and lower incisors were exposed.

NON-PTILODONTID ANTERIOR UPPER PREMOLARS

(Figure 15; Tables 21-23)

Of the non-ptilodontid species represented in the Roche Percee local fauna, anterior upper premolars have been previously recorded only for *Neoplagiaulax hunteri* (P1-3; see Simpson, 1936) and *Neoplagiaulax hazeni* (posterior fragment of P3; see Jepsen, 1940). The first and second upper premolars of *N. hunteri* and P3 (see Type G below) of *Neoplagiaulax*, cf. *N. hazeni* have been identified in the

Figure 15. Anterior upper premolars of non-ptilodontid multituberculates, Roche Percee local fauna, Saskatchewan, stereophotographic pairs: (A) occlusal view, UA 10792, Types A (top - length 0.7) and B (bottom - length 0.8), about x10; (B) occlusal view, UA 9978, Type C, length 0.8, about x10; (C) occlusal view, UA 10793, Type D, length 1.8, about x10; (D) occlusal view, UA 11675, Type E, length 1.7, about x11; (E) occlusal view, UA 10688, Type F, length 1.6, about x10; (F) occlusal view, UA 11652, Type G, length 1.7, about x11; (G) occlusal view, UA 11655, Type H, length 1.6, about x10; (H) occlusal view, UA 11645, Type I, length 1.7, about x10; (I) occlusal view, UA 10371, Type J, length 1.3, about x10; (J) occlusal view, UA 10783, Type K, length 1.2, about x10.

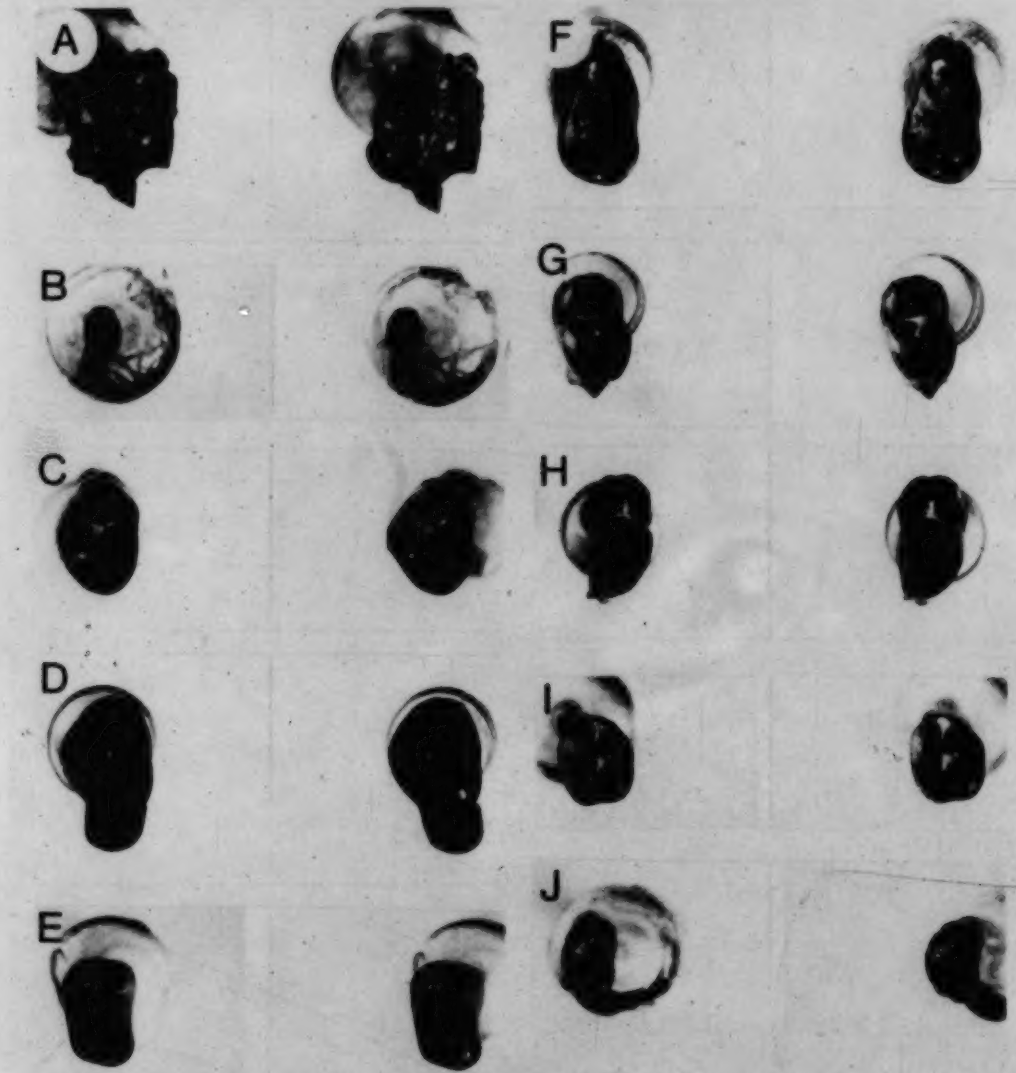

A
F
B
G
C
H
D
I
E
J

Table 21. Measurements and descriptive statistics of the anterior upper premolars of non-ptilodontid species in the Roche Percee local fauna, site UAR2a.

Type	Measurement	N	OR	M±SE	SD	CV
A	Length	5	0.7-0.8	0.78±.02	.04	5.7
	Width	5	0.6-0.7	0.62±.02	.04	7.2
B	Length	2	0.8-0.9	0.85±.05	.07	8.3
	Width	2	0.7	---	---	---
D	Length	12	1.6-1.8	1.71±.02	.08	4.6
	Width	13	1.2-1.5	1.34±.02	.08	5.7
E	Length	18	1.6-1.8	1.73±.01	.06	3.4
	Width	19	1.3-1.5	1.40±.02	.07	4.8
F	Length	13	1.6-1.8	1.68±.02	.07	4.3
	Width	14	1.1-1.3	1.21±.02	.07	6.0
G	Length	6	1.5-2.0	1.78±.07	.17	9.7
	Width	6	1.0-1.2	1.10±.04	.11	10.0
H	Length	5	1.6-1.9	1.74±.05	.11	6.6
	Width	5	1.1-1.3	1.20±.03	.07	5.9
I	Length	11	1.6-2.0	1.79±.03	.11	6.3
	Width	12	1.0-1.1	1.02±.01	.04	3.8
J	Length	2	1.3-1.4	1.35±.05	.07	5.2
	Width	2	1.1	---	---	---

Table 22. Measurements and descriptive statistics of the anterior upper premolars of non-ptilodontid species in the Roche Percee local fauna, site UAR2.

Type	Measurement	N	OR	M±SE	SD	CV
C	Length	1	0.8	---	---	---
	Width	1	0.5	---	---	---
D	Length	2	1.7-1.8	1.75±.05	.07	4.0
	Width	2	1.3-1.4	1.35±.05	.07	5.2
E	Length	1	1.6	---	---	---
	Width	1	1.3	---	---	---

Table 23. Measurements and descriptive statistics of the anterior upper premolars of non-ptilodontid species in the Roche Percee local fauna, site UAR2g.

Type	Measurement	N	OR	M±SE	SD	CV
A	Length	1	0.7	---	---	---
	Width	1	0.6	---	---	---
B	Length	1	0.8	---	---	---
	Width	1	0.7	---	---	---
D	Length	2	1.7-1.8	1.75±.05	.07	4.0
	Width	2	1.3	---	---	---
K	Length	1	1.2	---	---	---
	Width	1	0.8(est.)	---	---	---

Roche Percee sample, the latter with some indication of heterogeneity (perhaps P3's of *N. hunteri* are included). An attempt is made below to tentatively associate and assign anterior upper premolars of the remaining non-ptilodontid taxa, primarily on the basis of size and frequency correlation with the more well known parts of the dentitions. Formal allocation, however, is precluded until more nearly complete material is known. The approach taken by Clemens (1964, pp.97-99) to designate the individual phena of anterior upper premolars as 'Types', followed by a letter designation, is adopted here. Supposed deciduous premolars were identified as such by reference to Szalay (1965) and Lillegraven (1969).

DESCRIPTION

Type A.- Very small, two-rooted teeth with three cusps that are triangular in cross section and equidistantly spaced on the crown, one anteriorly and two posteriorly. These teeth are almost certainly P1's as evidenced by the anterior margin, which does not overlap the anterior root, the lack of an interdental wear facet on the anterior surface, and by the occurrence of a supposed P1 and P2 in the same maxillary fragment (UA 10792).

Type B.- Very small, two-rooted P2's, one of which occurs in the above-mentioned specimen (UA 10792) with P1. The three major coronal cusps are arranged in a triangle, one labially and two lingually. One specimen, UA 11647, has an additional cuspule developed anteroexternally.

__Type C__.- A single tiny, two-rooted tooth, the crown of which differs from the previous three types in being longer relative to its width and much lower. It bears four cusps (2:2) and is very likely a P3.

__Type D__.- Medium-sized, two-rooted P1's with three cusps, one posterolingual in position and the other two, which are lenticular in cross section and joined to about one-half their height, being oriented anterolingual-posterolabially. The crown is semicircular in occlusal outline, the lingual side being flat.

__Type E__.- Medium-sized, two-rooted P2's with one labial and two smaller lingual cusps. A ridge passes anteriorly from the labial cusp, then lingually and finally posteriorly to join the anterolingual cusp.

__Type F__.- Medium-sized, two-rooted P3's with three to five cusps (mode 4) and with an expanded posterior lobe. A ridge similar in development and position to that on premolars of Type E is present.

__Type G__.- Medium-sized teeth, thought to be deciduous P1's. The anterior face of the crown slopes gently and merges with the anterior root without an overhang as usually is seen on P2's and P3's. Three (one anterior and two posterior) or four (2:2) cusps may be present on the crown, which characteristically is inclined to one side on the root(s). No complete root(s) are preserved on these teeth but the short bases remaining indicate that only a single root supported the crown; however, it may have bifurcated distally as in Type H.

Type H.- Medium-sized teeth, thought to be deciduous P2's. Four (2:2) cusps dominate the crown. UA 10514, the only tooth of this type preserving a substantial part of the root, bears a single root that arises from the base of the crown but then bifurcates distally.

Type I.- Medium-sized teeth, thought to be deciduous P3's. The crowns are elongate and bear five (six in the case of UA 10522) cusps; a single low cusp on one end of the crown followed by (or preceded by, depending upon which end is anterior) two rows of two cusps each.

Type J.- Small to medium-sized, two-rooted teeth, probably P2's, with four (2:2) lenticular cusps placed on the crown, which is elliptical in occlusal view.

Type K.- A small to medium-sized, two-rooted tooth, probably a P1. The three coronal cusps are arranged in an equilateral triangle.

DISCUSSION

Because of their exceedingly small size Types A, B, and C (P1, P2, and P3, respectively) probably pertain to Mesodma sp. P and/or Mimetodon silberlingi. At any rate, Types A and B are referable to the same species because of their association in the same maxillary fragment (UA 10792).

Types D, E, and F are probably P1, P2, and P3, respectively, of Neoplagiaulax, cf. N. hazeni as they are the largest non-ptilodontid anterior premolars in the sample and are also the most common. Furthermore, the posterior fragment of P3 preserved in the type specimen (PU 14432) of N. hazeni does not differ appreciably from premolars of Type F.

The lack of long, stout, well-formed roots on Types G, H, and I and the general coronal shape and topography (see Szalay (1965) and Lillegraven (1969)) lends support to the inference that these are deciduous teeth. Again, based on size-frequency data, these three types may well be deciduous precursors of Types D, E, and F.

The small to moderate size and infrequency in the sample of Types J and K suggest that these teeth may be referable to Microcosmodon conus and/or Ectypodus, cf. E. powelli, but there is no evidence to suggest which.

The possibility, of course, exists that one or more of the above 'Types' belong to a species not represented in the sample by any other tooth position or that more than one species may be included in a single 'Type'.

PART II. POSTCRANIAL OSTEOLOGY OF *PTILODUS KUMMAE* AND OTHER MULTITUBERCULATES

A) Previous Work on Multituberculate Postcrania

In 1909 Gidley reported the discovery of an incomplete skeleton associated with the skull and lower jaws of *Ptilodus montanus* from the Torrejonian of Montana. Bones of the postcranium described by Gidley include a cervical and a few caudal vertebrae, a phalanx, and fragments of a humerus, radius, ulna, femur, tibia, fibula, pelvis, and metapodials. Broom (1914) originally disputed Gidley's identification of the pelvis and proposed instead that the elements represented a pectoral girdle. However, in an addendum to the same paper, W. Granger, at Broom's request, confirmed Gidley's original interpretation. From the same specimen, Simpson (1926) analyzed locomotory and feeding habits and Jerison (1973) provided estimates, which have since been criticized by Radinsky (1975), for the body length and weight of *Ptilodus*.

An excellent specimen of the hind limbs and pelvis of an undetermined species of *Eucosmodon* was recovered from Puercan deposits in New Mexico and was referred to preliminarily in several reports (Granger, in Broom, 1914; Granger, 1915; Simpson, 1928a). Simpson and Elftman (1928), from a reconstruction of the hind limb and pelvic musculature, made inferences concerning the habits of *Eucosmodon* sp., and Granger and Simpson (1929) added a detailed osteological description of the specimen. Simpson (1937a) briefly compared the postcranial osteology of *Ptilodus* and *Eucosmodon*.

Recent discoveries by the Polish-Mongolian Palaeontological Expeditions to the Upper Cretaceous Djadokhta and Barun Goyot formations of Mongolia include incomplete postcrania of at least three species of multituberculates (Kielan-Jaworowska, 1970, 1974): *Kryptobaatar dashzevegi* Kielan-Jaworowska (1970); *Chulsanbaatar vulgaris* Kielan-Jaworowska (1974); and *Nemegtbaatar gobiensis* Kielan-Jaworowska (1974). Detailed descriptions of these specimens are forthcoming, but Kielan-Jaworowska (1969) has already reported the presence of epipubic bones in the skeleton of *K. dashzevegi*.

Less complete skeletons and isolated elements of allotherian postcrania have been identified by various authors and are listed below.

1) Cope (1882a) - an astragalus and caudal vertebrae of *Taeniolabis taoensis* (Cope, 1882a). The astragalus, redescribed and figured by Cope in 1884a, was later shown by Matthew (1937) to probably belong to a condylarth (it is, at least, undoubtedly therian). However, Cope (1884a) also described and figured a humerus and ulna of the same

species; Matthew (1897, 1937) did not discuss these. Although I have not studied the specimens firsthand, Cope's figures (1884a, pl.XXIIIc, figs. 3 and 4; 1884b, fig. 4b,c) appear to illustrate a humero-ulnar articulation of the condylar type possessed by multituberculates (see Jenkins, 1973).

2) Cope (1882b) - the distal extremity of a humerus of Meniscoessus conquistus Cope, 1882b (figured by Cope, 1884b, fig. 7g, and Cope, 1888, fig. 9g).

3) Marsh (1889) - a scapula, interclavicle, astragalus, and calcaneum of Camptomus amplus Marsh, 1889. Not all of Marsh's identifications have been accepted (Simpson, 1928a, b; McKenna, 1960b, 1961). McKenna (1961) agreed that the calcaneum and astragalus are allotherian but questioned the identification of the interclavicle and provisionally referred the scapula, the type of C. amplus, to the Marsupialia. Marsh (1889) also figured the distal end of a humerus of "Dipriodon lunatus" (Marsh, 1889), a left semilunar, probably of "Dipriodon robustus" (Marsh, 1889), and the proximal end of a femur of "Halodon sculptus" (Marsh, 1889). All three species are now referred (see Clemens, 1964) to Meniscoessus robustus (Marsh, 1889). The humerus and femur are undoubtedly allotherian; the semilunar does not resemble the bone tentatively identified as a semilunar of Ptilodus kummae (see below).

4) Simpson (1928c, p.9) - "several associated foot

bones, five fragmentary vertebrae, the lower end of a scapula, a large part of a humerus, ribs, and several other fragments" associated with the type skull of Djadochtatherium matthewi Simpson (1925) from the Upper Cretaceous Djadokhta Formation of Mongolia.

5) Granger and Simpson (1929) - several skeletal fragments of Stygimys teilhardi (Granger and Simpson, 1929) including fragments of both ulnae and femora, the right humerus and ilium, the left tibia, a phalanx, and lumbar, sacral, and caudal vertebrae.

6) Simpson (1937c, p.737) - "Skull,...with associated femur, ulna, and some other fragments" of Ptilodus montanus. The postcranial remains include left and right femora, a lumbar vertebra, a proximal fragment of a phalanx, and the distal end of a left humerus; no ulna is present. The femora are definitely allotherian, the phalangeal fragment is much too large to belong to the same individual, and the humeral fragment, as Deischl (1964) previously noted, belongs to a therian.

7) McKenna (1960b, 1961) - redescribed the fragmentary scapulocoracoid of Djadochtatherium and described two partial scapulocoracoids from the Upper Cretaceous Lance Formation of Wyoming, designating the latter as "Lance Type 1" and "Lance Type 2." Clemens (1964), on the basis of size and frequency, provisionally allocated the Lance Type 1 and Type 2 scapulocoracoids to Mesodma formosa and Cimolodon

nitidus Marsh, 1889, respectively (the scapulocoracoid illustrated by Jouffroy and Lessertisseur (1967, fig. 11) is that of *Mesodma formosa*?, not *Djadochtatherium* as labelled).

8) Deischl (1964) - scapulocoracoids, humeri, ulnae, radii, pelves, femora, tibiae, calcanei, and astragali from a large sample from the Upper Cretaceous Bug Creek Anthills locality, Hell Creek Formation variously assigned, on the basis of size and frequency data, to *Mesodma thompsoni*, *Mesodma formosa*, *Cimexomys minor*, *Cimolodon nitidus*, *Stygimys kuszmauli* Sloan and Van Valen, 1965, and *Catopsalis joyneri* Sloan and Van Valen, 1965.

9) Deischl and Sloan (in Sloan and Van Valen, 1965) - isolated elements of *Mesodma thompsoni*.

10) Sahni (1972) - distal part of a humerus referred to *Mesodma*, proximal fragment of a femur of *Mesodma*? *primaevus* (Lambe, 1902), and calcanea of *Mesodma*? *primaevus* and *Meniscoessus major* (Russell, 1937).

11) Jenkins (1973) - a left ulna (unidentified) and a right humerus referred to cf. *Catopsalis*, both from the Hell Creek Formation of Montana.

B) Materials and Methods

Unfortunately, prior to discovery of the type specimen (UA 9001), the skull, both lower jaws, several anterior vertebrae, the pectoral girdles, the greater part of the forelimbs, and some caudal vertebrae had weathered out and were displaced for a short distance along an erosional crevice descending from the skeleton. Fragments of these anterior elements were recovered by surface collecting and by washing and screening the surrounding rock matrix. The identifiable fragments obtained in this manner include several teeth (left i1 and P4; right p4, m1, and P2-4), the distal end of the right scapulocoracoid, fragments of the right humerus, proximal parts of both radii, a proximal segment of the right ulna, ten phalanges, and three caudal vertebrae. Association of the isolated elements with the articulated specimen cannot be subject to question owing to the close proximity in which they were found, the virtual absence of bone in the immediately surrounding area, the anatomical correspondence to comparable allotherian skeletal elements previously described (especially those of _Ptilodus montanus_ described by Gidley (1909)), the absence of duplication of anatomical positions, and the close fit of some of the articular surfaces of apposing elements with each other (for example, the humerus and ulna).

The specimen, as preserved _in situ_, was lying on its right side, which was the first side to be prepared. When prepared, the right side was covered by a white moldmaking rubber (Silastic A RTV, Dow Corning Corp.). The specimen was then inverted and the left side prepared, a mold made, photographs taken, and finally embedded in a liquid casting plastic (Bio-plastic, Ward's Natural Science Establishment, Inc.). This technique firmly secured the fragile and delicate bones and permitted observation of both sides of the specimen. During preparation, several of the bones were removed because they prevented preparation of more critical areas of the skeleton. Bones removed for this purpose include: left calcaneum, left ectocuneiform, left metatarsal V, three phalanges of the left pes, a parafibula? (see below), and several smaller fragments, primarily pedal sesamoids.

The articulated portion of the skeleton is virtually complete posterior to the anterior part of the rib cage (Figs. 16, 17). The only portions of the pectoral limbs remaining intact are a poorly preserved distal segment of the right? radius?, most of the right? carpus (with attached metacarpal and complete digit I and the proximal portion of metacarpal II), and some middle and distal phalanges of the left? manus. The tail was obviously very long and had curled around the anterior part of the body. A central segment of the tail, containing at least six vertebrae, had weathered out prior to discovery.

Although the specimen (UA 9001) of Ptilodus kummae is

Figure 16. Ptilodus kummae, n. sp. (UA 9001): left side of nearly complete postcranial skeleton. CD (followed by number) - caudal vertebrae, E? - epipubic? bone, L (followed by number) - lumbar vertebra, LFE - left femur, LFI - left fibula, LIS - left ischium, LT - left tibia, MP - manual phalanges, PP - pedal phalanges, RA - right astragalus, RCM - right calcaneum, RCS - right carpus, RFE - right femur, RFI - right fibula, RT - right tibia, S (followed by number) - sacral vertebra. About x1.5.

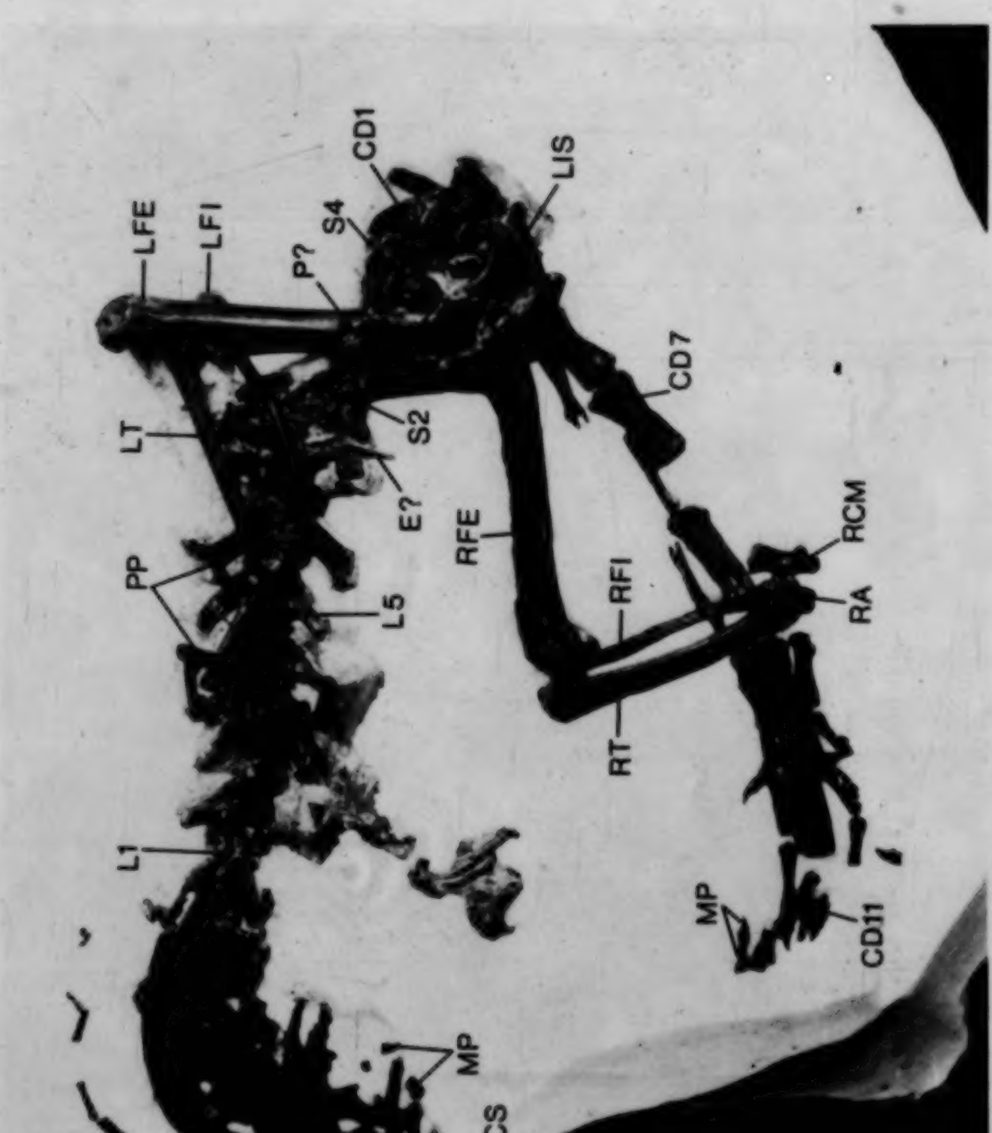
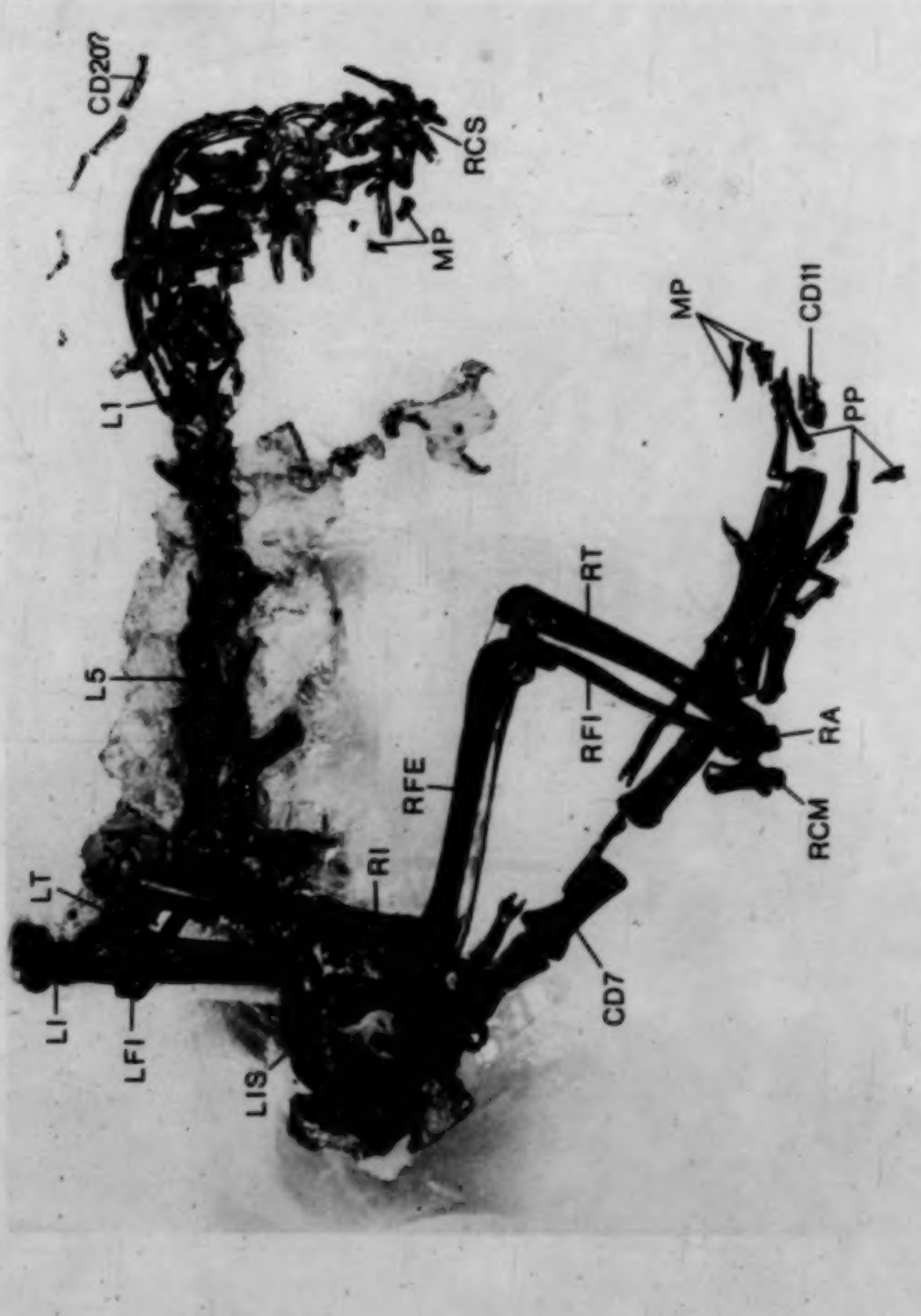

LFE
LFI
P?
S4
CD1
LIS
LT
S2
E?
CD7
PP
L5
RFE
RFI
RCM
RA
RT
L1
MP
CD11
MP
RCS
CD20?

Figure 17. Ptilodus kummae, n. sp. (UA 9001): right side of nearly complete postcranial skeleton. CD (followed by number) - caudal vertebra, L (followed by number) - lumbar vertebra, LFI - left fibula, LI - left ilium, LIS - left ischium, LT - left tibia, MP - manual phalanges, PP - pedal phalanges, RA - right astragalus, RCM - right calcaneum, RCS - right carpus, RFE - right femur, RFI - right fibula, RI - right ilium, RT - right tibia. About x1.6.


CD20??
RCS
MP
L1
MP
CD11
PP
L5
RT
RFI
RA
RFE
RCM
RI
LT
LI
LFI
LIS
CD7

virtually complete postcranially, certain elements are either incomplete, crushed, or were not recovered. Comparative material of all the known articulated postcranial remains, and many disarticulated and fragmentary bones, of North American multituberculates was available for this study. Structural features exhibited by these comparative materials, but not by UA 9001, are also described below. For each bone, or series of bones (in the case of vertebrae), a description of UA 9001 followed by a description of other, but more complete or better preserved, specimens of that element, or series of elements, is provided. It is essential to emphasize, however, that structural identity of the various postcranial elements of different multituberculate taxa is not implied by this procedure; it is simply intended to provide an outline of what may have been the basic structural plan, at least for ptilodontoids and taeniolabidoids. It appears that, generally, the amount of structural variability in known postcranial bones between ptilodontoid and taeniolabidoid species is not great.

Comparative materials described, or otherwise used in this study, are as follows:

a) USNM 6076 - incomplete skeleton, *Ptilodus montanus*, Gidley Quarry, Fort Union Formation, Montana.

b) AMNH 16325 - incomplete skeleton, *Eucosmodon* sp., Nacimiento Formation, New Mexico.

c) UMVP 1414 - ulna, *Mesodma formosa*?, Bug Creek

Anthills site, Hell Creek Formation, Montana.

d) UMVP 1417 - ischial fragment, Mesodma formosa?, Bug Creek Anthills site, Hell Creek Formation, Montana.

e) UA 11992 - distal fragment of right scapulocoracoid, unidentified multituberculate, Bug Creek Anthills site, Hell Creek Formation, Montana.

f) UA 11994 - distal fragment of humerus, unidentified multituberculate, Bug Creek Anthills site, Hell Creek Formation, Montana.

g) UA 11995 - proximal fragment of tibia, unidentified multituberculate, Bug Creek Anthills site, Hell Creek Formation, Montana.

h) UA 11996 - parafibula?, unidentified multituberculate, Bug Creek Anthills site, Hell Creek Formation, Montana.

i) UA 11300 - distal fragment of humerus, Ptilodus kummae, site UAR2g, Ravenscrag Formation, Saskatchewan.

j) UA 11302 - ulnar fragment, Ptilodus kummae, site UAR2g, Ravenscrag Formation, Saskatchewan.

k) UA 11301 - proximal fragment of femur, Ptilodus kummae, site UAR2g, Ravenscrag Formation, Saskatchewan.

(C) DESCRIPTION

(i) Osteology of the Postcranial Axial Skeleton

(a) Thoracic Series

UA 9001.- If the number of lumbar vertebrae is correctly interpreted at seven (see below), then there are preserved in UA 9001 seven posterior thoracic vertebrae; the more anterior thoracics were not recovered. The preserved thoracic vertebrae are variously disarticulated, crushed, and fragmented (Figs. 18, 19).

The centra in the posterior part of the thoracic series are platycoelous. The anterior articular end of each centrum is transversely elongate, almost rectangular in outline, and its concavity, although shallow, is situated along the ventral half of the articular surface; the dorsal half is almost flat and ascends obliquely anterodorsally. The posterior articular end is almost circular in outline, except for a slight dorsal flattening, and is shallowly concave. The lateral margins of the anterior end extend anteriorly for a short distance and articulated with a laterally rounded facet on each side of the posterior end of the preceding centrum.

Cranial costal foveae, or demifacets, are clearly visible on the ventrolateral margins of the anterior ends of the fourth from last and antepenultimate thoracic vertebrae.

Figure 18. *Ptilodus kummae*, n. sp. (UA 9001), stereophotographic pair: dorsal view of thoracic and lumbar vertebral series. L (followed by number) - lumbar vertebra. About x2.1.

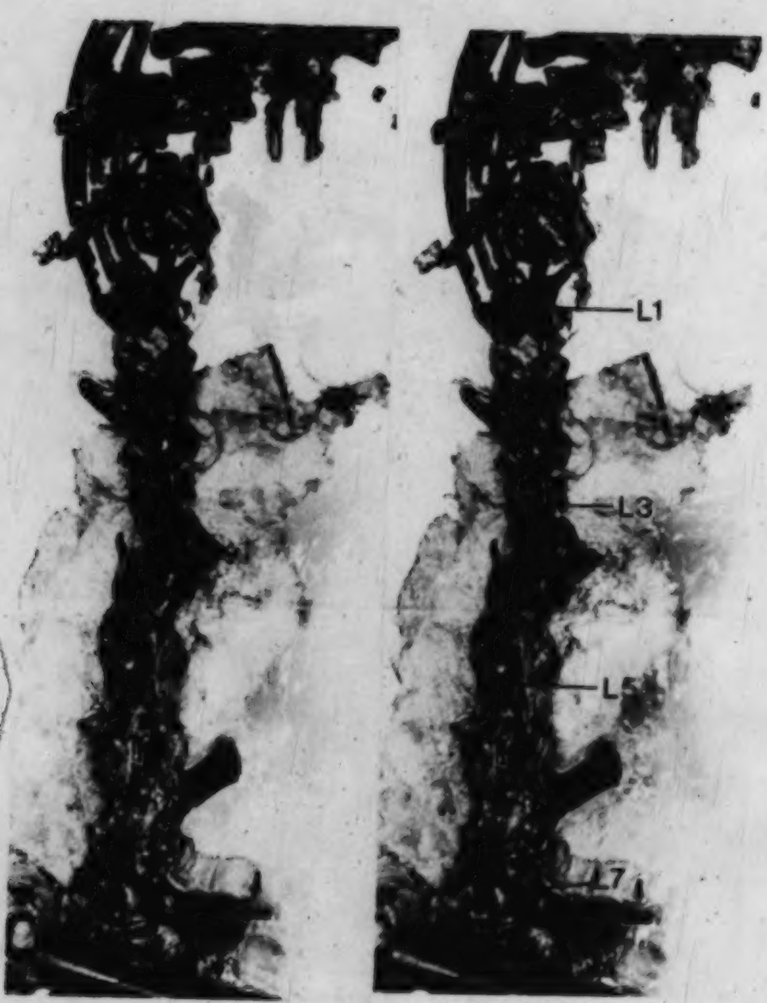
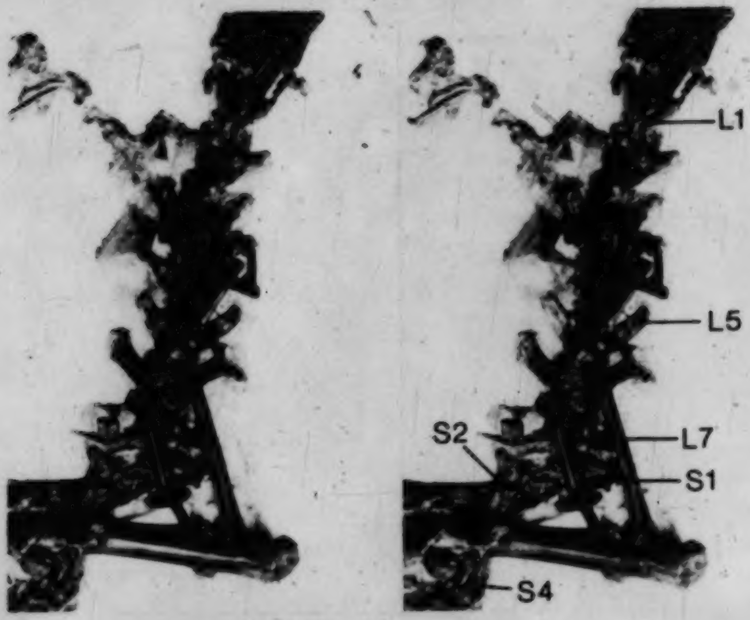

L1
L3
L5
L7

Figure 19. *Ptilodus kummae*, n. sp. (UA 9001), stereophotographic pair: ventral view of thoracic, lumbar, and sacral vertebral series. L (followed by number) - lumbar vertebra, S (followed by number) - sacral vertebra. About x1.3.


L1
L5
S2
L7
S1
S4

The terminal thoracic vertebra is tentatively identified as such by the presence of a less clear and smaller cranial demifacet.[1]

Two shallow fossae, separated by a median crest, or keel, mark the ventral surface of each of the thoracic centra of UA 9001.

The pedicles on each of the preserved thoracic vertebrae are shorter than the lamina and the vertebral canal is consequently transversely elliptical in frontal section. The laminae of the ultimate and what is taken to be the penultimate thoracic vertebrae each give rise sagittally to a low anterodorsally directed spinous process, or neural spine. The spine of each thoracic vertebra is of moderate length and is triangular in cross section, the acute-angled apex of the triangle being situated along the ventral margin. It appears that, in normal standing posture, the spinous processes, at least far posteriorly in the thoracic series and anteriorly in the lumbar series, were of low enough inclination to be wedged between the posterodorsally directed postzygapophyses of the preceding vertebra in a tongue-in-groove arrangement. The spinous process of the antepenultimate thoracic vertebra is more vertically inclined and the anticlinal vertebra is probably the fourth from last thoracic. The variation in size and attitude of the spinous processes of the remaining, more anterior thoracic vertebrae cannot be determined as the spines are either crushed or broken away.

---

[1] The presence or absence of ribs is the traditional criterion employed for differentiation between the thoracic and lumbar regions (e.g. Todd, 1922; Schultz and Straus, 1945; Schultz, 1961) and is also used here. Other workers (e.g. Washburn and Buettner-Janusch, 1952; Ankel, 1967) prefer to delimit the two series by the orientation of the zygapophyses, the change always occurring within a single vertebra, that is, the "diaphragmatic vertebra". This vertebra bears thoracic zygapophyses anteriorly and lumbar zygapophyses posteriorly. Ankel (1967) has called this vertebra the "anticlinal vertebra" but this is in contrast to Slijper's (1946) usage of the terms anticlinal and diaphragmatic vertebrae, the former indicating intermediacy of orientation of the neural spine, the latter intermediacy of zygapophyseal orientation. Slijper's terminology is adopted here.

The zygapophyses are developed as prominent, protuberant processes, the prezygapophyses facing ventrolaterally, the postzygapophyses dorsomedially. Low ridges, one passing anteriorly from the dorsal aspect of each postzygapophysis, converge along the dorsolateral margins of the neural spine, and meet at the spine's distal terminus. The prezygapophyseal facets are concave, the postzygapophyseal ones convex.

The diapophyses of the thoracic vertebrae are developed on the lateral walls of the pedicles as low, horizontal ridges that provided articulation for the rib tubercles. A small, short process directed posteriorly arises from the reduced diapophysis on at least the second-, third-, and fourth-from-last thoracic vertebrae; none appears to be developed on the last thoracic.

(b) Lumbar Series

UA 9001.- The lumbar vertebrae, with the exception of the first, are tightly articulated with one another (Figs. 18, 19). The pleurapophyses, directed anteroventrolaterally, become progressively longer and wider posteriorly and less pointed, that is, more truncate, distally.

The seventh lumbar vertebra is markedly different from the preceding six in that the pleurapophyses were positioned perpendicular to the sagittal plane.

Mid-ventral keels are, as on the thoracic vertebrae, developed on the lumbars, at least anteriorly. In anteroposterior sequence the lumbar vertebrae become increasingly longer and wider, with the exception of L 7, which is shorter but still wider than L 6 (see Table 24). From L 1 to L 7 the spinous processes become more slender and more erect (but still inclined anterodorsally), and the zygapophyses become more robust.

Other Material.- The spinous processes on the known lumbar vertebrae of *Eucosmodon* sp. (Granger and Simpson, 1929) are much more vertical in orientation than are those of *P. kummae*. This feature, as well as the well developed pleurapophyses, indicate that the lumbar vertebrae known in the specimen of *Eucosmodon* sp (AMNH 16325) are probably well posterior in the series.

Table 24. Measurements of vertebrae of UA 9001 (*Ptilodus kummae*, n. sp.).

Vert.	Length Pre- to Postzyga.	Length Centrum	Width Prezyga.	Width Postzyga.	Width Tr. Processes
L 1	7.3*	---	5.4*	4.4	7.8*
L 2	8.4*	---	5.7*	4.4*	10.3*
L 3	---	---	---	4.7*	10.4*
L 4	8.2*	---	6.1	5.1*	---
L 5	8.3*	---	6.2*	5.8*	13.6*
L 6	9.1*	---	---	---	14.9*
L 7	7.9*	---	7.0*	6.2*	19.0*
S 1	---	---	---	---	11.0*
S 2	---	---	---	---	8.9*
Cd 1	---	3.9*	---	---	8.8*
Cd 2	6.2	---	5.6	4.5	---
Cd 3	6.0	---	5.7	4.4	10.7*
Cd 4	6.3	---	5.6	4.1	10.4*
Cd 5	8.1	---	4.4*	2.3*	9.9*
Cd 6	---	8.5*	---	---	9.2*
Cd 7	---	10.7*	---	---	8.0*
Cd 8	---	11.0*	---	---	---
Cd 9	---	11.2*	---	---	---
Cd 10	---	11.3*	---	---	---
Cd 16?	---	8.4*	---	---	---
Cd 18?	---	6.9	---	---	---
Cd 19?	---	6.2	---	---	---

Table 24. (continued)

Cd 20?	---	5.5	---	---	---
Cd 21?	---	5.0	---	---	---
Cd 22?	---	4.1	---	---	---
Cd 23?	---	3.4	---	---	---
Cd 24?	---	2.9*	---	---	---

*approximate

(c) Sacral Series

UA 9001.- The first sacral vertebra is slightly shorter than the terminal lumbar and bears short and stout transverse processes (Fig. 19). The transverse processes are directed laterally and slightly posteriorly. In ventral view, the anterior half of the terminus of each process of S 1 is flat and parasagittal in orientation; the posterior half is concave and is directed posteromedially. The ventral surface of the centrum is essentially flat; posteriorly the centrum expands slightly transversely to accommodate the centrum of S 2. The fusion between the centra of S 1 and S 2 appears to have been incomplete as they are disarticulated in UA 9001.

The second sacral vertebra is less robust than S 1 and is firmly synostosed with S 3. The transverse processes of S 2 are oriented obliquely anterolaterally and probably contacted the posterolaterally directed transverse processes of S 1, thereby jointly providing an auricular facet for articulation with the ilia. A prominent pair of ventral foramina occur side by side near mid-length on the centrum of S 2.

The position of the line of fusion between S 2 and S 3 is unclear but it is thought to be just anterior to the transverse processes, which are short and project anterolaterally, of S 3. As preserved, the bulk of S 3 and its articulation with the next posterior centrum are obscured ventrally by the proximal end of the left femur, which overlies them. Dorsally, although the posterior sacral vertebrae are quite fragmented, it appears that the centrum of S 3 is fully fused with the next posterior one, indicating that the specimen has four sacral vertebrae.

At least on S 3 and S 4 a prominent median sacral crest is developed dorsally. The centrum of S 4 is elongate and relatively narrow transversely. Its transverse processes are broken away but, from their bases, an anterolateral orientation is indicated. A prominent ventral foramen is developed just posterior to mid-length and just to the right of sagittal on S 4; posterior and lateral to this foramen are developed paired and smaller foramina, one on the posterior part of the base of each transverse process. A fragmentary haemal arch is preserved in association with the posteroventral margin of the centrum of S 4. The distal parts of the two prongs of the arch are broken away but, proximally, the prongs are joined by a crescentic crosspiece, presumably homologous to the intercentrum and primitively present in the tails of reptiles (Romer, 1956).

(d) Caudal Series

UA 9001.- Lessertisseur and Saban (1967) have separated the caudal series into two types of vertebrae; anterior caudals and posterior caudals, the latter of which lack vertebral arches and have reduced or rudimentary processes. The transition is gradational, however, and, although not all of the details of the anterior caudals can be seen, it is thought that the specimen of P. kummae possessed at least five, probably six, anterior caudal vertebrae.

The transverse processes of Cd 1 to Cd 5 arise from almost the entire length of the centra and are pointed distally (Fig. 20A). In dorsal view, the anterior margins of the transverse processes of Cd 1 are oriented obliquely anterolateral-posteromedially. On succeeding caudal vertebrae the anterior margin becomes progressively more perpendicular to sagittal in orientation. The posterior margin of the transverse processes of all anterior caudals are slanted anterolateral-posteromedially. A foramen pierces the posterior base of each transverse process of at least Cd 1, Cd 5, and Cd 6; this area is not visible on Cd 2-4.

The centrum of Cd 1 is only slightly longer than its width. The remaining anterior caudal vertebrae become progressively longer, the most rapid increase occurring between Cd 4 and Cd 5 (see Table 24). The articular ends of the centra of Cd 1 to Cd 6 are not clearly visible. The zygapophyses of Cd 1 to Cd 4 are large and well developed; on Cd 5 they are reduced and on Cd 6 the prezygapophyses are reduced, the postzygapophyses rudimentary. The prezygapophyseal facets on the anterior caudals face dorsomedially, are slightly concave, and articulate with the

Figure 20. Ptilodus kummae, n. sp. (UA 9001), stereophotographic pairs: (A) dorsal view of sacral and caudal vertebral series, about x2.2, and (B) caudal vertebrae in, from top to bottom, lateral, dorsal, and ventral views, respectively, about x4.1. CD (followed by number) - caudal vertebra, HS - haemal spine, S (followed by number) - sacral vertebra.

CANADIAN THESES
ON MICROFICHE

30729

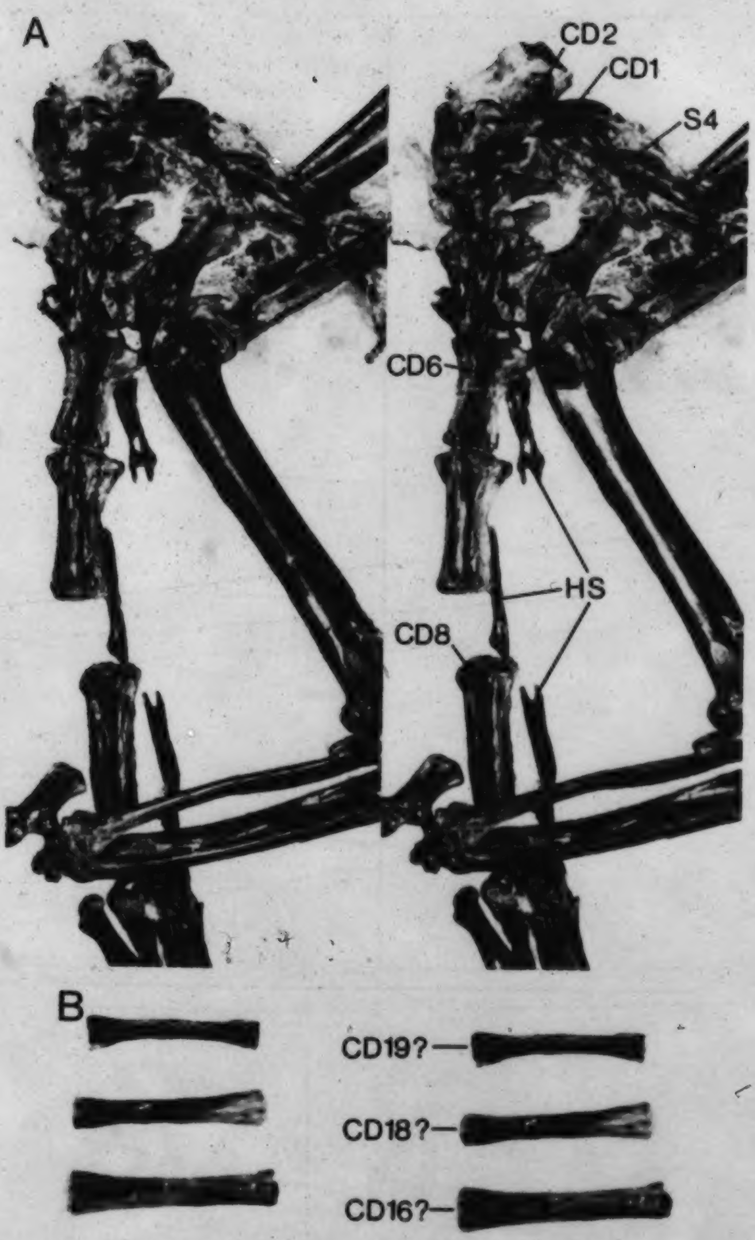
THÈSES CANADIENNES
SUR MICROFICHE

AUTHOR/AUTEUR

KRAUSE, D.W.

TITLE/TITRE

PALEOCENE MULTITUBERCULATES
(MAMMALIA, ALLOTHERIA)...


A
CD2
CD1
S4
CD6
HS
CD8
B
CD19?
CD18?
CD16?

postzygapophyses, which, correspondingly, face ventrolaterally and are slightly convex. A deep, U-shaped notch separates the postzygapophyses posteromedially. The notch separating the prezygapophyses anteromedially is in the shape of an open V. The spinous processes of Cd 2 to Cd 6 are centrally located along the dorsal length of the centra, are nearly vertical in orientation, and decrease progressively in height posteriorly such that the spinous process of Cd 6 is merely an elongate, low, sagittal crest. The neural spine of Cd 1 is hidden from view as Cd 1 was displaced after death to a position beneath Cd 2.

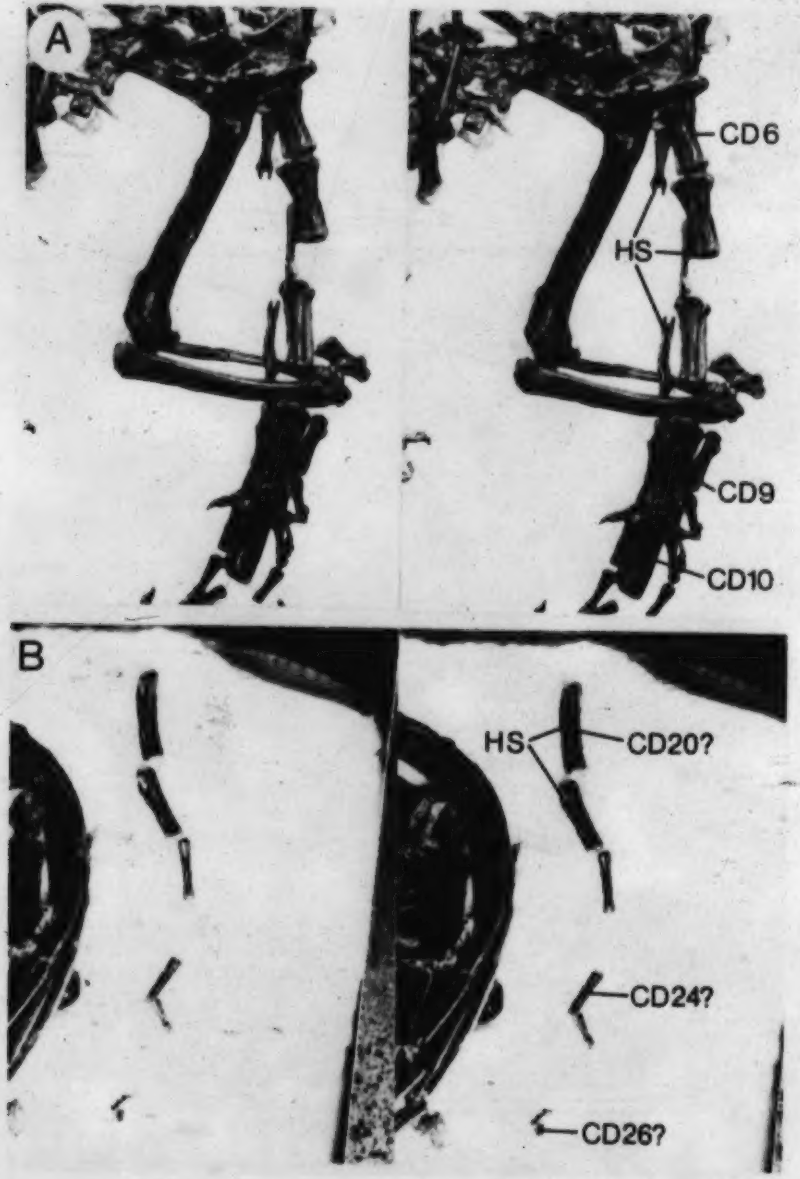
The haemal arches ventral to the anterior caudal vertebrae are relatively large and well developed. The canals formed between the intercentra and the arches are triangular in cross section, the apices being directed ventrally. The haemal spines between Cd 1? and Cd 2? and between Cd 2? and Cd 3? (the spines are somewhat displaced from the centra) are laterally compressed, spatulate in side view, and were slightly less than perpendicular to the centra in orientation. Further posteriorly, the spines become progressively less perpendicular, projecting anteroventrally until, as seen on Cd 14? and more posterior caudals, the arches are parallel to the centra. The haemal arches and spines situated between the centra of Cd 3 to Cd 6 are either not preserved in UA 9001 or are hidden from view by the overlying ischia. The haemal spine between Cd 6 and Cd 7 differs from those described above in being dorsoventrally depressed and spatulate, rather than laterally compressed and spatulate. The distal terminus of the haemal spine of Cd 6 is evenly rounded in ventral profile.

The number of caudal vertebrae can only be estimated. The first four complete proximal posterior caudal vertebrae preserved in UA 9001 (an anterior fragment of the fifth (Cd 11) is also present) are still very slightly increasing in length posteriorly, that is, the longest caudal vertebra is posterior to or is Cd 10 (Figs. 20A, 21). If this is so, and considering the lengths of the 21 preserved caudal vertebrae (see Table 24), it can be estimated that the tail of the specimen was probably between 160 and 180 mm long and had 24 to 28 vertebrae (probably about 26).

On Cd 7 to Cd 10 are developed paired rudimentary prezygapophyses, rudimentary transverse processes, small paired processes anteroventrally, and a low, elongate spinous process, all of which decrease in size posteriorly. The centra are elongate and cylindrical, expanding slightly at their extremities. The intercentra and haemal arches on Cd 7 to Cd 10 exhibit trends initiated in the anterior caudal vertebrae, which have been described above. The haemal spines, however, beginning at Cd 7 bear a U-shaped notch sagittally on the distal terminus, rather than being evenly rounded as on Cd 6.

The positions of the three caudal vertebrae recovered

Figure 21. _Ptilodus_ _kummae_, n. sp. (UA 9001), stereophotographic pairs: (A) ventral view of proximal caudal vertebrae, about x1.2, and (B) ventral view of distal caudal vertebrae, about x2.2. CD (followed by number) - caudal vertebra, HS - haemal spine.


A
CD6
HS
CD9
CD10
B
HS
CD20?
CD24?
CD26?

by washing and screening are uncertain. However, for ease of reference, the three vertebrae will be referred to as Cd 16?, Cd 18?, and Cd 19?, which should be close approximations of their correct positions (Fig. 20B). Their lengths, or estimated lengths, are given in Table 24. The processes and crests observed on Cd 7 to Cd 10 are only slightly developed on these caudals. In lateral view, the centra are dorsally convex and ventrally concave. The primary difference from Cd 7 to Cd 10, however, is that the haemal arches are firmly fused to the centra. The haemal arches are symmetrical; both anteriorly and posteriorly a deep, mid-ventral, U-shaped notch is incised.

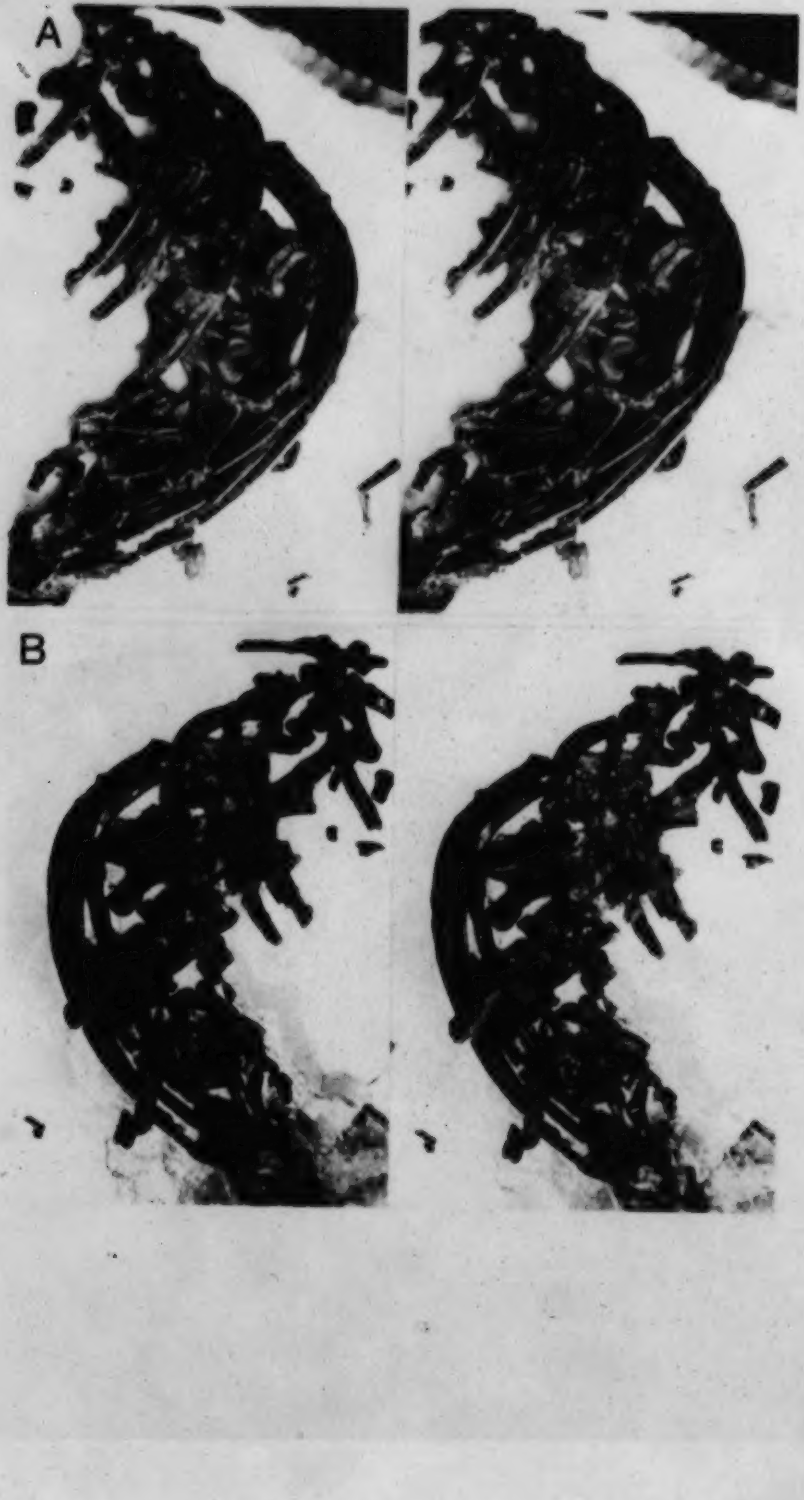
The terminal segment of the tail is preserved in UA 9001 and the individual centra are tentatively labelled as Cd 20? to Cd 26? (Fig. 21B). Haemal arches are preserved on Cd 20? to Cd 23?. Unlike Cd 16?, Cd 18?, and Cd 19?, however, the arches are not fused to the centra and are exceedingly delicate structures that lie parallel to and beneath the centra. The posterior mid-ventral, U-shaped notch is much deeper than the anterior notch on Cd 20? and Cd 21?; on Cd 22? and Cd 23? the notches are equally deep.

Other Material.- Structurally very similar to those of *P. kummae*, the known caudal vertebrae of *Eucosmodon* sp. (AMNH 16325 - Granger and Simpson, 1929) and *Stygimys teilhardi* (AMNH 16024 - personal observation) are relatively large and robust and indicate rather large and heavy tails for all three taxa.

(e) Ribs

UA 9001.- Fragments of at least fifteen ribs, belonging to both left and right sides, are preserved in UA 9001 (Fig. 22). Several ribs are nearly complete, well preserved, and exhibit a conformation of typically mammalian aspect. The head, or capitulum, is separated from the tuberculum by a neck and the body of the rib is elliptical in cross section. The more anterior ribs (exact positions cannot be ascertained) have a longer neck region and a less open dorsolateral "angle". The ribs exhibit a longer elliptical cross section at the angle in the more anterior ribs. The surficial area of the tubercular facet is larger than that of the capitulum in all of the preserved fragments.

Figure 22. Ptilodus kummae, n. sp. (UA 9001), stereophotographic pairs: (A) left side, about x2.3, and (B) right side, about x2.1, showing fragmentary ribs.


A
B

(ii) Osteology of the Appendicular Skeleton

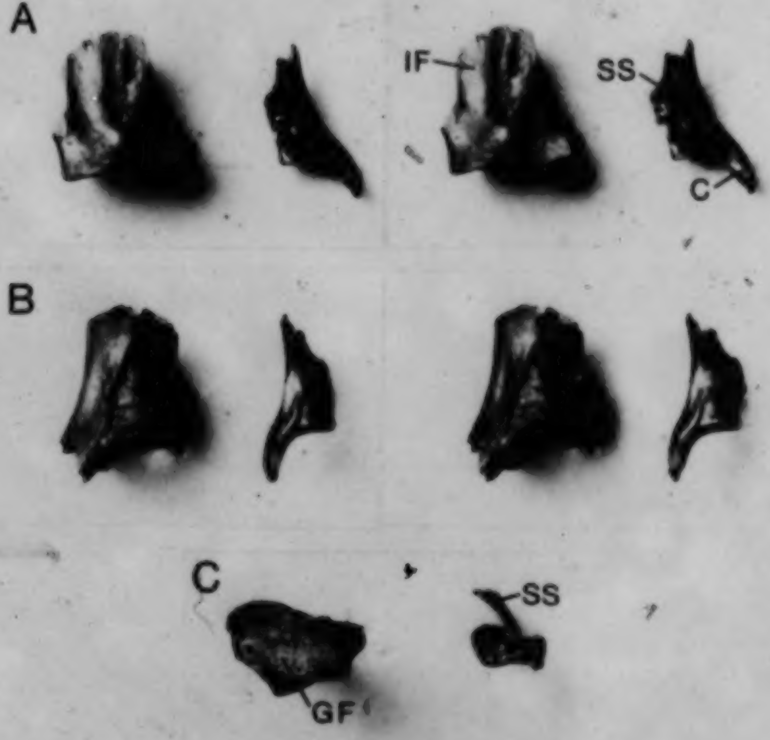
(a) Scapulocoracoid

UA 9001.- The right scapulocoracoid is represented by a small distal fragment from which all or most of the fused coracoid has been broken away (Fig. 23). The size of the area of breakage indicates that the coracoid was large relative to that of most therian mammals. The glenoid fossa is shallow and, in ventral outline, is pyriform, being broad and obliquely flattened along the posterior surface and tapered gradually towards the coracoid.

The ventral base of the scapular spine is situated about 1.1 mm above the lateral border of the glenoid fossa but, immediately dorsal to its origin, sweeps anterodorsally to become the cranial border of the scapular blade. The supraspinous fossa is ~~therefore~~ limited to a small area dorsal to the coracoid, as in other known multituberculate scapulocoracoids (see McKenna, 1961, figs. 1-3). The infraspinous fossa of UA 9001 is relatively expansive and, although the more proximal parts of the blade are not preserved, presumably occupied almost the entire lateral surface.

On the costal surface of the scapula is developed a low ridge that parallels the cranial border and extends from near the medial rim of the glenoid fossa posterodorsally for

Figure 23. Scapulocoracoids of Ptilodus kummae, n. sp. (UA 9001 - left) and unidentified multituberculate, Hell Creek Formation (UA 11992 - right) in (A) lateral (stereophotographic pair), (B) medial (stereophotographic pair), and (C) ventral views. C - coracoid, GF - glenoid fossa, IF - infraspinous fossa, SS - scapular spine. About x4.8.


A
IF
SS
C
B
C
SS
GF

approximately 3 mm. A shallow, elliptical fossa, carrying a foramen near its center, is developed posterolaterally on the costal surface. Its posterodorsal limits cannot be determined because of breakage.

Other Material.- UA 11992, a right scapulocoracoid of an unidentified multituberculate from the Hell Creek Formation, has the entire coracoid preserved (Fig. 23). The coracoid is indistinguishably synostosed to the scapula, is transversely expanded to a slight degree distally, and, together with the glenoid fossa of the scapula, provided a large articular arc (approximately 90°) to receive the head of the humerus.

A large part of the distal portion of the scapular spine, but not the acromion process, is preserved on UA 11992. The spine projects laterally and then posteriorly, transcribing a broad quarter-circular arc (in frontal section) and thereby providing an extensive area for muscle attachment anterolaterally.

(b) Humerus

UA 9001.- For descriptive clarity the humerus will be treated as if lying in a horizontal plane, as in non-cursorial mammals in general (Jenkins, 1971b), such that the elbow and shoulder joints are at or near the same level.

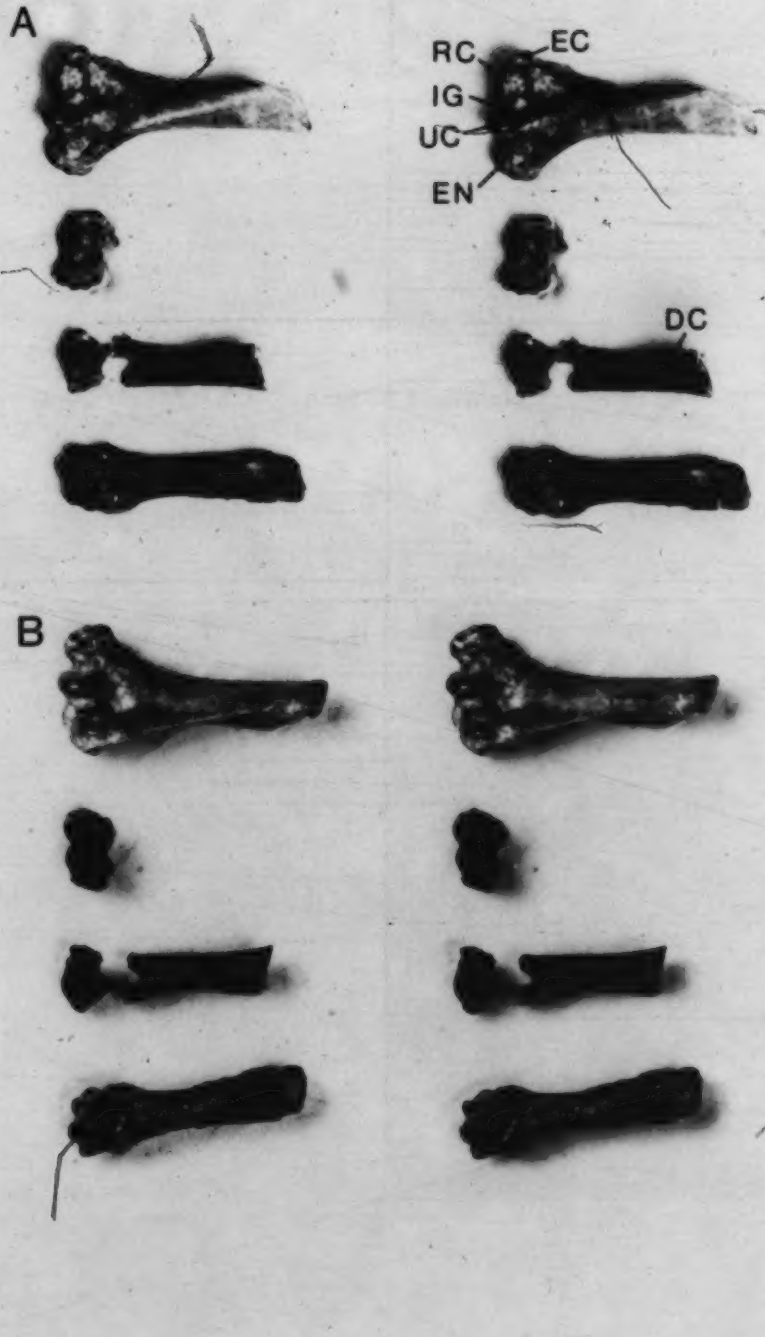
The humeral head is represented by four small fragments that provide little information. The size and curvature of the hemispherical head indicate that it does not belong to the femur, a conclusion that is supported by comparison with the humeral head of USNM 6076, the specimen of P. montanus from Gidley Quarry. Furthermore, both femora have been completely preserved in UA 9001.

The diaphysis is incomplete, but the fragment recovered shows that the humerus is moderately short and stout (Fig. 24). The deltopectoral crest is developed ventrolaterally. Proximally, the crest produces an acute-angled corner on the shaft; distally, the crest assumes a more ventral position and becomes indistinct. At approximately mid-length on the dorsal surface of the diaphysis two small, distally-directed nutrient foramina are developed. A shallow groove extends proximally for about 2.4 mm from each foramen.

Distally the shaft expands laterally, giving rise to a prominent ectepicondylar crest, which is not preserved in its entirety. The ectepicondyle is well developed and extends well out from the radial condyle.

The radial condyle (capitulum) is large and spherical ventrally and extends as a broad linear ridge onto the dorsal surface. Ventrally, a shallow groove separates the radial condyle from the ectepicondyle. The ulnar condyle, separated from the radial condyle by the wide intercondylar groove, is elongate and wraps around the distal end of the

Figure 24. Multituberculate humeri in (A) ventral, and (B) dorsal view, stereophotographic pairs: Top - unidentified multituberculate, Hell Creek Formation (UA 11994); second from top - *Ptilodus kummae*, n. sp. (UA 11300); second from bottom - *Ptilodus kummae*, n. sp. (UA 9001); bottom - *Ptilodus montanus* (USNM 6076). DC - deltopectoral crest, EC - ectepicondyle, EN - entepicondyle, IG - intercondylar groove, RC - radial condyle (capitulum), UC - ulnar condyle. About x2.2.


A
RC
EC
IG
UC
EN
DC
B

humerus. The extensor surface, situated dorsally, is oriented proximolaterally; its flexor surface, situated ventrally, proximomedially.

Other Material.- The olecranon fossa is not preserved on the humeral fragment of UA 9001. However, UA 11300, a distal humeral fragment of *P. kummae* from the same site (UAR2g), shows that the fossa was deep and perforate, as it is in *P. montanus* (USNM 6076).

The linear ulnar condyle, in distal view, intercepts the interepicondylar axis at an angle of approximately 72° on UA 11300 as well as on the humeral fragment of *P. montanus* (USNM 6076). The entepicondyle is not preserved on either UA 9001 or UA 11300 but a distinct groove separates it from the ulnar condyle. More nearly complete humeri of multituberculates recovered from the Hell Creek Formation in UMVP and UA collections (for example, UA 11994, see Fig. 24) show that on these the entepicondyle is much larger than the ectepicondyle, and that it projects distomedially as a broad, dorsoventrally depressed flange of bone and bears a well developed entepicondylar foramen (see also Jenkins, 1973, fig. 19).

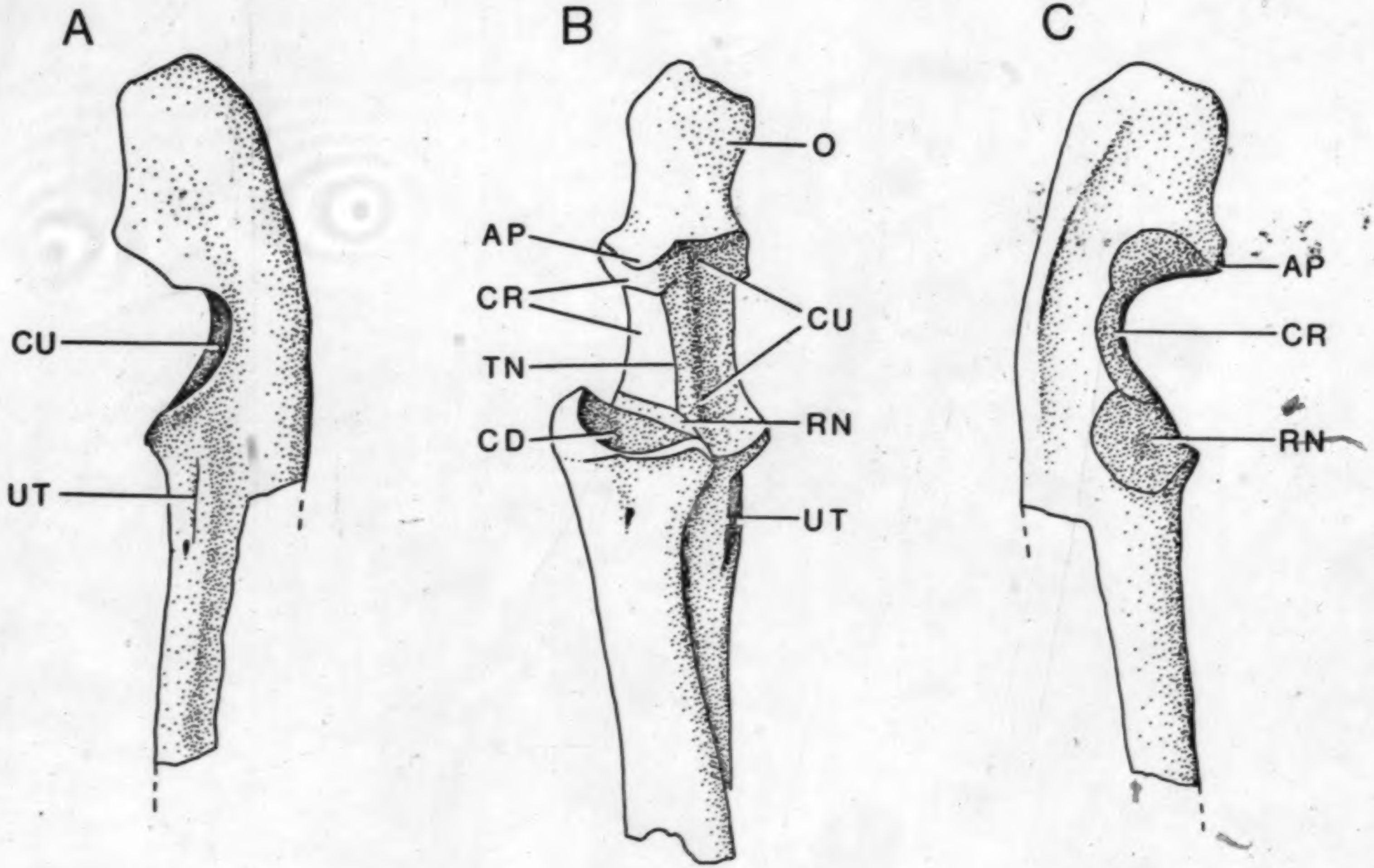
(c) Ulna

UA 9001.- The right ulna is represented by a small proximal fragment broken slightly dorsal to the radial notch; the left ulna, or fragments thereof, was not recovered.

The olecranon is four-sided, laterally compressed, and extends approximately 3.5 mm dorsal to the proximal rim of the semilunar notch (Fig. 25). At its posterodorsal apex the olecranon is inclined medially. The articular surface for the radial condyle of the humerus is presented as a prominent flange on the dorsolateral corner of the semilunar notch. Distally, this articular surface is less expanded laterally and extends to the top of the radial notch. The ulnar condyle of the humerus is accommodated by a smooth, deeply concave, articular surface on the ulna, which proximally is expanded medially by a thin shelf but distally is narrower and occupies the medial two-thirds of the semilunar notch. The proximodistal axis of the facet for the ulnar condyle is obliquely oriented (estimated at about 10°) to the ulnar shaft. The articular surfaces for the ulnar and radial condyles on the ulna are separated by a prominent ridge, the trochlear notch, which is oriented slightly obliquely (proximolateral-distomedially) to the axis of the ulnar shaft and articulates with the intercondylar groove on the humerus. The trochlear notch is extended proximoanteriorly into a well developed anconeal process that fitted into the olecranon fossa of the humerus when the elbow joint was extended.

Other Material.- UA 11302, an ulnar fragment of P.

Figure 25. Ptilodus kummae, n. sp. (UA 9001): camera lucida diagram of reconstructed ulna (UA 9001 and UA 11302) in (A) medial, (B) anterior (with radius of UA 9001 added to show articular relationship), and (C) lateral view. AP - anconeal process, CD - capitular depression, CR - articular surface for radial condyle of humerus, CU - articular surface for ulnar condyle of humerus, O - olecranon, RN - radial notch, TN - trochlear notch, UT - ulnar tuberosity. About x8.8.


A
B
C
CU
UT
AP
CR
TN
CD
O
CU
RN
UT
AP
CR
RN

kummae from site UAR2g preserving the distal half of the semilunar notch and a large part of the shaft, affords the following description and contributes, along with UA 9001, to the reconstruction in Fig. 25.

The radial notch, which articulated with the articular circumference of the radius, is a large, shallow, concave facet distal to the articular surface for the radial condyle and both lateral and distal to the articular surface for the ulnar condyle of the humerus.

Distal to the semilunar notch the shaft of the ulna becomes narrower transversely. Just below the articular surface for the ulnar condyle and medially on the shaft, a raised longitudinal ridge, the ulnar tuberosity, borders a lateral depression. A nutrient foramen is situated at the ventral base of this depression.

The ulnae of UA 9001 and UA 11302 are not preserved distally but the shaft of a single specimen (UMVP 1414) from the Hell Creek Formation, described and tentatively referred to Mesodma formosa by Deischl (1964), is complete except for the distal articular surface. Near mid-length, the diaphysis is, in cross section, in the shape of an isosceles triangle, the base being situated anteriorly and the apex at the posterior border. Distally the shaft arches posteriorly and becomes much smaller in diameter and cylindrical.

(d) Radius

UA 9001.- The head of the radius is irregularly elliptical in dorsal outline and is higher posterolaterally than anteromedially (Figs. 25B, 26). The shallowly concave, oval capitular depression articulates with the radial condyle of the humerus. The articular circumference of the radial head is developed for approximately 180° peripheral to the capitular depression except anteriorly. A flat area on the radial head, developed lateral and peripheral to the capitular depression, articulated with the shallow groove that separates the ectepicondyle from the radial condyle on the distal end of the humerus.

The shaft is obliquely compressed such that its greatest diameter is in an anteromedial-posterolateral plane. The radial tuberosity is developed distal to the neck on the posterior surface and is high and crested, running down the longitudinal axis of the shaft. Distal and somewhat anterior to the radial tuberosity an interosseus crest is developed, but its distal extent cannot be determined because of breakage. A small nutrient foramen is developed anteriorly on the neck of the radius.

A crushed segment of a long bone is preserved proximal to the right? manus of UA 9001 (Fig. 27). The distal end is expanded and it is for this reason that it is presumed to belong to the radius.

Figure 26. Ptilodus kummae, n. sp. (UA 9001): (A) posterior, (B) anterior, and (C) dorsal view of proximal fragment of right radius. AC - articular circumference, CD - capitular depression, IC - interosseus crest, RT - radial tuberosity. About x4.9.

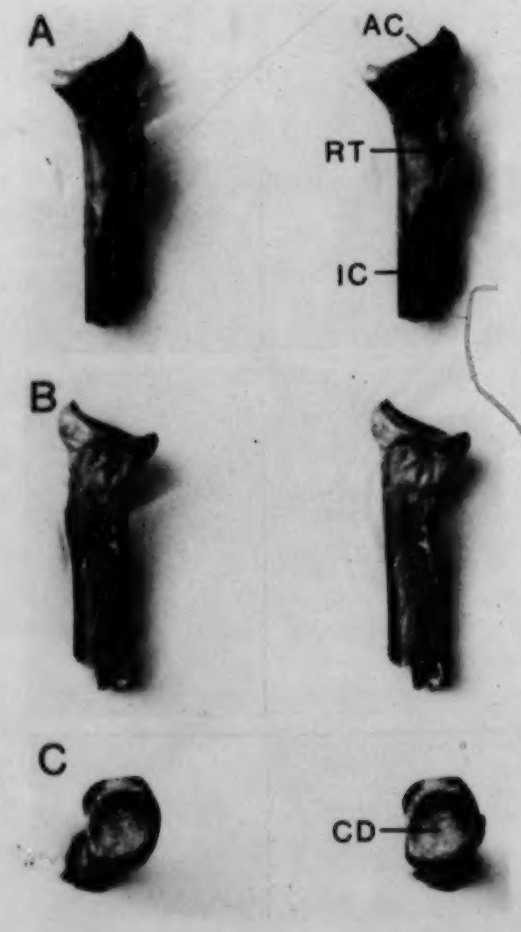
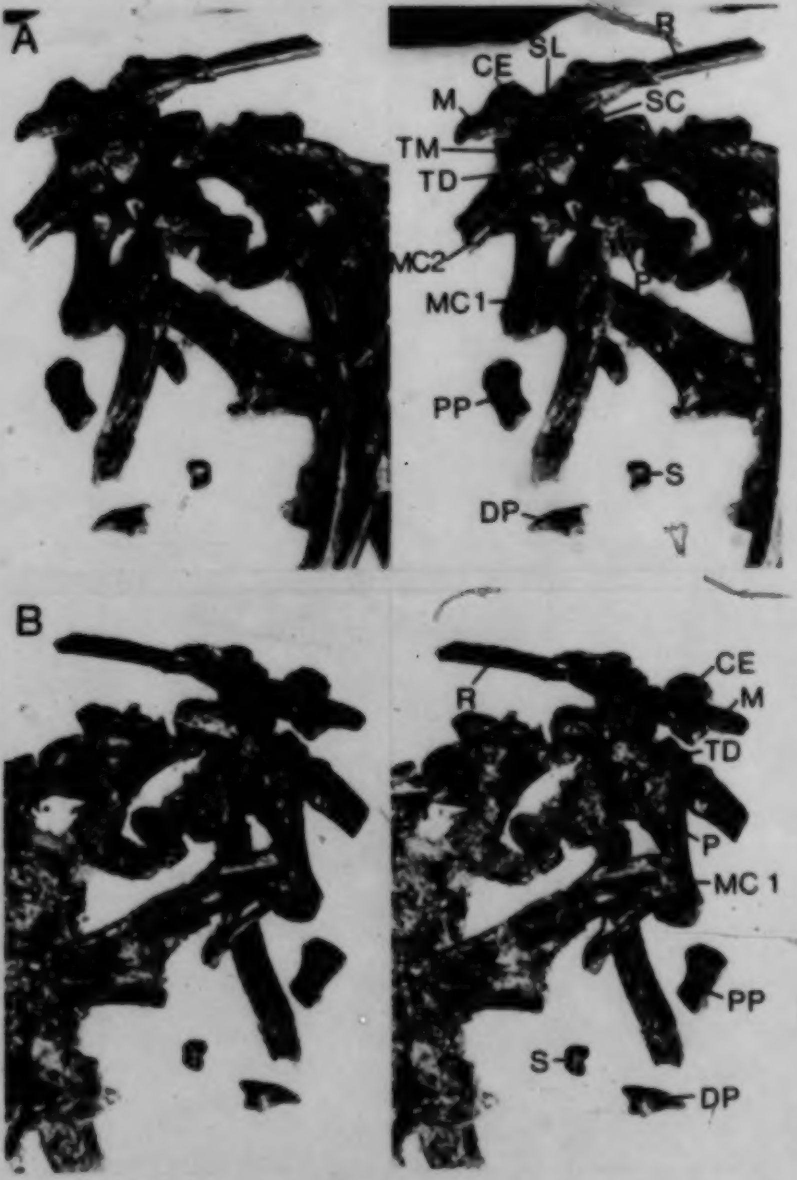

A
AC
RT
IC
B
C
CD

Figure 27. *Ptilodus kummae*, n. sp. (UA 9001), stereophotographic pairs (A) dorsal (about x4.4), and (B) ventral (about x4.2) view of right manus. CE - centrale, DP - distal phalange, M - magnum, MC (followed by number) - metacarpal, P - prepollex, PP - proximal phalange, R - radius, S - sesamoid, SC - scaphoid, SL - semilunar, TD - trapezoid, TM - trapezium.


A
R
SL
CE
M
SC
TM
TD
MC2
P
MC1
PP
S
DP
B
CE
M
R
TD
P
MC 1
PP
S
DP

(e) Carpus

UA 9001.- Identification of the individual carpal bones must be considered to be very tentative, inasmuch as 1) carpal bones have previously not been described for any multituberculate, neither are they well known for any other non-therian fossil mammal (Jenkins and Parrington, 1976), or, for that matter, cynodonts (Jenkins, 1971a); 2) the carpal bones of UA 9001 are slightly disarticulated, especially laterally; 3) at least two of the carpalia of the preserved carpus were not recovered; 4) details of most of the articular facets are indistinct or are hidden from view; and 5) most importantly, the orientation of the manus cannot be confidently determined. The dorsal and ventral surfaces of the manus were identified from the metacarpals and from the dorsally convex aspect of several of the carpals, and is reasonably certain. However, whether the preserved carpus belongs to the right or left side is the critical problem. Tentatively, the carpus of UA 9001 is considered to be a right one for the following reasons: 1) the complete metacarpal preserved on the left side of the manus appears to have been articulated with only two phalanges in proximodistal sequence, therefore identifying that digit as the pollex; 2) the distal end of a badly crushed long bone attached to the left side of the proximal carpal row is thought to be the radius (see above); and 3) the three carpals preserved in the distal row each appear to be articulated with a single metacarpal. If these metacarpals belong to the right wrist they are, in mediolateral sequence, the trapezium, trapezoid, and magnum (Fig. 27). This leaves the unciform to attach to digits IV and V, which is usually the case in mammals (Lessertisseur and Saban, 1967) (it is, however, unknown if multituberculates, like many therapsids, retained all five distal carpals). The following description assumes the above interpretation to be correct. The elongate bone to the left of the carpus is, therefore, a prepollex (radial sesamoid), and not the pisiform, as would be the case if the manus was a left one.

The only preserved elements of the proximal row of carpal bones are the semilunar and scaphoid; the cuneiform and, if present in life, the pisiform have not been recovered. The scaphoid is a large bone, of irregular shape, that distomedially bears a distinct semicircular facet for articulation with the trapezium. Proximolaterally, the scaphoid articulated with the semilunar; distolaterally, with the centrale. Slight contact may have also been possible between the scaphoid and trapezoid bones but no articular facets are visible.

The semilunar is a very small, wedge-shaped bone situated proximolateral to the scaphoid, proximomedial to the centrale, distal to the radius, and, presumably, medial to the cuneiform.

The centrale, a rectangular bone located between the proximal and distal rows of the carpus, is an elongate bone whose long axis is dorsoventral in orientation, and which is strongly convex proximally and strongly concave distally. Its articulations are presumed to have been as follows: with the cuneiform proximolaterally and laterally, the semilunar proximomedially, the scaphoid medially, and the magnum distally.

The trapezium, the furthest medial of the distal carpalia, is roughly equivalent to the trapezoid in size and, in dorsal view, is quadrilateral in shape, its distal margin being longer than, but parallel to, the proximal margin. It articulated distally with metacarpal I, laterally with the trapezoid, and proximally with the scaphoid. Its articular relationship with the prepollex is vague.

The trapezoid articulated directly with metacarpal II but also contacted the proximolateral corner of metacarpal I. Laterally, a broad, flat, vertical facet articulated with the magnum and, medially, the contact with the trapezium is an oblique one. In dorsal view, the trapezoid assumes the shape of an equilateral, right-angled triangle, the hypotenuse being situated proximomedially.

The magnum is very similar to the centrale in shape, being convex proximally, concave distally, and dorsoventrally elongate. Its distal articular surface is undivided and articulated with metacarpal III, although slight contact with the proximolateral border of metacarpal II was maintained. Both the magnum and centrale have very large, flat articular facets on their lateral surfaces, for articulation with the unciform or perhaps with both the unciform and cuneiform. The fact that the lateral facets are more or less continuous across the two bones may indicate that they articulated with only a single medial facet on the unciform and that the unciform, therefore, was relatively large.

The prepollex is an elongate bone that is expanded at both ends. The proximal expansion, which articulated with both the trapezium and the pollical metacarpal, is the larger of the two. The prepollex measures 2.8 mm in length and is therefore slightly greater than one-half the length of metacarpal I.

Three small, fragmented pieces of bone occur ventral to the carpus as preserved. These may be other sesamoid bones, rib or vertebral fragments, or even fragments of carpalia; the evidence does not permit a choice.

(f) Metacarpus

UA 9001.- Preserved with the right carpus of UA 9001 is a complete metacarpal I (5.3 mm in length) and the proximal portion of metacarpal II (Fig. 27). Four metapodial fragments were also obtained by washing and screening the immediately surrounding rock matrix but more precise identification of the bones was not possible.

Although not preserved distally, metacarpal II was more slender and probably longer than the pollical metacarpal. The base of metacarpal I is expanded and large, much more so than the base of metacarpal II. The distal terminus of metacarpal I is also expanded. The proximal juxtaposition of metacarpals I and II appears to have been slightly less in life than as preserved in UA 9001 but the divergent angle between the two metacarpals was still approximately 35°. The angle between metacarpal I and the prepollex cannot be resolved owing to the postmortem displacement of the latter.

(g) Manual phalanges

UA 9001.- Both distal (ungual) and proximal phalanges of digit I are associated in the right manus (Fig. 27). The proximal phalanx is 2.6 mm long and, at mid-shaft, is 1.1 mm in width. Both the proximal base and, to a lesser extent, the distal head are expanded relative to the transverse diameter of the shaft. The base is dorsoventrally expanded. The head, in dorsal profile, is very slightly convex, bearing no median furrow.

The distal phalanx is 2.4 mm long. The proximal articulation is strongly concave in side view. The flexor tubercle is low, rounded, and is offset from the articular surface by a notch that carries a large nutrient foramen, which is directed anteriorly. The ungual process, which supported the claw, is slightly recurved and, dorsomedially and dorsolaterally, exhibits a longitudinal fissure, the dorsolateral one being longer and deeper. In dorsal view, the ungual process is constricted near mid-length, then expands distally, and finally tapers to a rounded apical edge.

A small sesamoid bone loosely associated with digit I may have articulated ventral to the metacarpal-phalangeal joint or ventral to the interphalangeal joint. Its large size indicates that it was probably associated with the former.

Three middle and three distal phalanges are preserved near the tip of the right hind foot. Whether these phalanges belong to the right or left forefoot is unknown but that they are manual phalanges is certain, by process of elimination; all ten digits of the hind limbs are preserved in their entirety in UA 9001. Also, six proximal or middle phalanges and one distal phalanx were recovered by washing and screening the immediately surrounding matrix. These too are almost certainly from the manus. Without precise identification of the phalanges, i.e., to which digit they belong, description is somewhat meaningless. It can, however, be noted that the distal phalanges are longer (2.7 to 3.2 mm) than the distal phalanx of digit I of the right manus.

(h) Pelvis

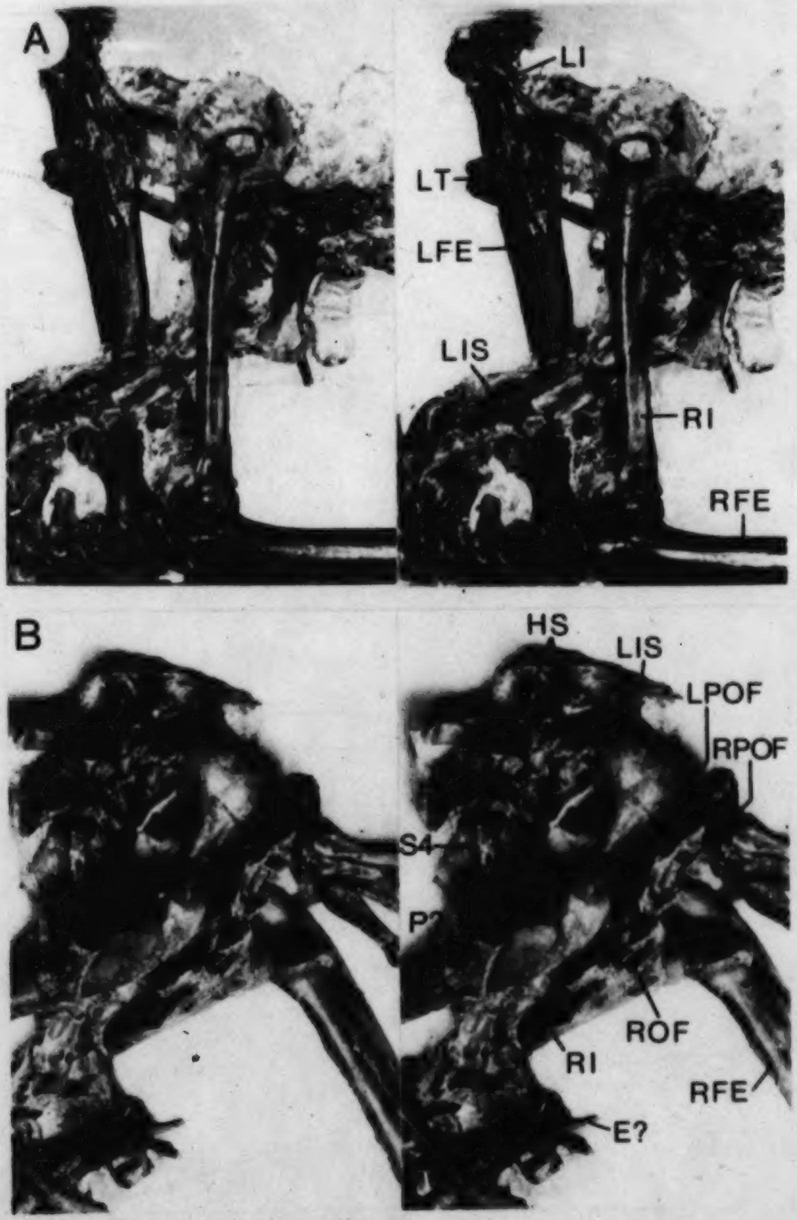
UA 9001.- Both ilia of UA 9001 are preserved intact, as is most of the left ischium; the right ischium and both pubes are crushed (Fig. 28). None of the pelvic bones are retained as separate elements but, rather, are fully synostosed to each other.

The ilium is long and rod-like and, anteriorly, curves laterally. Medially it is expanded at the auricular surface. Posterior to the sacroiliac union the ilium is elliptical in cross section but expands again, both dorsally and ventrally, near the anterior rim of the acetabulum. The ventral expansion, the iliopubic eminence, is large and imperceptibly merges with the pubis. Details of the acetabula are hidden by the tight articulation with the femoral heads. It does appear, however, that the acetabulum is not completely bounded by bone dorsally and that it was directed dorsolaterally, as in other known multituberculate pelves.

The ischium, just posterior to the acetabulum, is, in cross section, flat laterally and rounded medially. The dorsal margin is arciform, concave anterodorsally. The caudal margin is strongly convex posteriorly. Posterior to the acetabulum the ventral margin of the ischium descends posteroventrally.

The distortion of the pubes and the right ischium (the

Figure 28. *Ptilodus kummae*, n. sp. (UA 9001), stereophotographic pairs: (A) dorsomedial view of left innominate, medial view of right ilium (about x1.9), and (B) dorsolateral view of left ischium, ventral view of right innominate (about x2.3). E? - epipubic? bone, HS - haemal spine, LFE left femur, LI - left ilium, LIS - left ischium, LPOF - left post-obturator foramen, LT - left tibia, P? - parafibula?, RFE - right femur, RI - right ilium, ROF - right obturator foramen, RPOF - right post-obturator foramen, S (followed by number) - sacral vertebra.


A
LI
LT
LFE
LIS
RI
RFE
B
HS
LIS
LPOF
RPOF
S4
P?
ROF
RI
RFE
E?

ventral part of the left ischium is covered on both sides by overlying bone) makes structural interpretation difficult but it appears certain that posterior to the obturator fenestra there is another, smaller fenestra, hereafter referred to as the post-obturator fenestra. Although sutural contacts between the individual pelvic bones have synostosed and therefore provide no topographic markers, the anterior fenestra is probably the homologue of the obturator fenestra of other mammals and cynodonts by virtue of its position and its large size, both of which are inconclusive and, therefore, tentative criteria in this instance.

The obturator fenestra is situated directly ventral to the acetabulum, its anterior margin being situated at approximately the same level as the anterior margin of the acetabulum. Ventrally, it is bounded by a thin strap of bone, which has not been preserved in any other multituberculate specimen. Deformation precludes precise measurement of the margins of the obturator fenestra although its anteroposterior length appears to have been close to 4 mm.

The post-obturator fenestra is separated from the obturator fenestra by a plate of bone measuring approximately 2.0 mm long (anteroposteriorly). The fenestra itself is approximately 2.5 mm long and about 2.0 mm high. Although breakage has occurred, it appears that, ventrally, the post-obturator fenestra was rimmed by a very thin and delicate strap of bone.

The cranial ramus of the pubis descends posteroventrally, thereby forming the anterior border of the obturator fenestra. Ventrally, the pubis swings posteriorly to form the ventral border. No distinct articular facets for the epipubic bones are evident on the pubes, primarily because of deformation.

The epipubic bones are elongate, slender, boomerang-shaped bones (Fig. 28B) that are strikingly similar to bones tentatively identified as clavicles of *Eozostrodon* by Jenkins and Parrington (1976). One is located near the right ilium; the other, near the left ischium. The possibility of the clavicles alone having drifted posteriorly to the pelvic region, while the rest of the pectoral appendages appear to have remained anteriorly, is small.

Other Material.- The ilia of *Eucosmodon* sp. (see Granger and Simpson, 1929) and *Kryptobaatar dashzevegi* (see Kielan-Jaworowska, 1969) are basically similar to those of *P. kummae*. Unlike the ilium of *P. kummae*, however, that of *Eucosmodon* sp. is, anteriorly, compressed transversely.

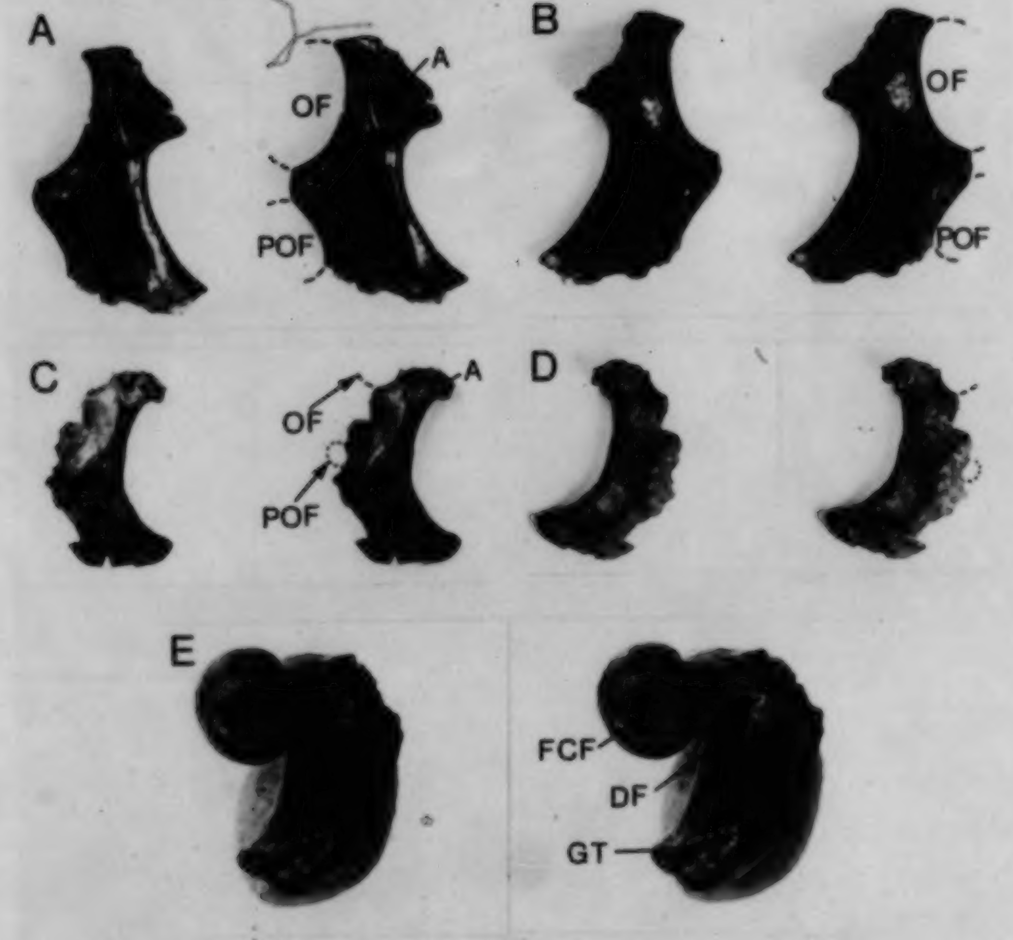
The presence of two fenestrae in each innominate of multituberculates is also borne out by several specimens of unidentified multituberculates from the Hell Creek Formation and by the specimen of *Eucosmodon* sp. (AMNH 16325).

In UMVP 1417 (see Fig. 29A, B), for instance, a left ischial fragment from the Hell Creek Formation assigned to *Mesodma formosa* by Deischl (1964), the concave dorsal margins of both fenestrae are preserved. The fenestrae are separated by a cylindrical bony rod of small diameter. The ventral margins of the fenestrae are not preserved.

In AMNH 16325 (see Fig. 29C, D), the specimen of *Eucosmodon* sp., the dorsal outlines of the obturator fenestra are well preserved and correctly depicted by Simpson and Elftman (1928, figs. 1,2) and Granger and Simpson (1929, figs. 19,20). The ischium is broken ventrally but along the line of breakage there is a small, dorsally concave margin that is not broken; it is a natural edge of bone and represents the dorsal border of the post-obturator fenestra (this observation has been independently corroborated by R.C. Fox, B.G. Naylor, and H.-D. Sues). The fenestra is apparently enclosed entirely within the symphyseal region, a position that is even more confusing in functional considerations. It is further possible that the post-obturator foramen was not bounded by bone ventrally, as it is in *P. kummae*.

As recontructed by Kielan-Jaworowska (1969, fig. 2, but not fig. 3C) the dorsal indentation in the pelvis of *Kryptobaatar dashzevegi* along the ventral rim of the ischium and posterior to the obturator foramen may represent the post-obturator fenestra but, again, it may not have been

Figure 29. Stereophotographic pairs: (A) lateral (about x6.3), and (B) medial (about x6.5) view of left ischial fragment (UMVP 1417), Mesodma formosa?, Hell Creek Formation; (C) lateral (about x1.1), and (D) medial (about 1.1) view of left ischial fragment (AMNH 16325), Eucosmodon sp., Nacimiento Formation; and (E) posteroventromedial (about x4.0) view of proximal fragment of left femur (UA 11301), Ptilodus kummae, n. sp.. A - acetabulum, DF - digital fossa, FCF - fovea capitis femoris, GT - greater tuberosity, OF - obturator foramen, POF - post-obturator foramen.


A
A
OF
POF
B
OF
POF
C
A
OF
POF
D
E
FCF
DF
GT

rimmed by bone ventrally. Since my observations of the specimen of Kryptobaatar are based entirely upon Kielan-Jaworowska's (1969) figures my conclusions about the pelvic structure are therefore necessarily conservative. Forthcoming detailed descriptions of the postcrania of Kryptobaatar and other multituberculates may shed light on the above inferences, although the presence of a post-obturator foramen in one or more species of multituberculates does not necessarily indicate that it is universally present, or at least well-developed, in all members of the order.

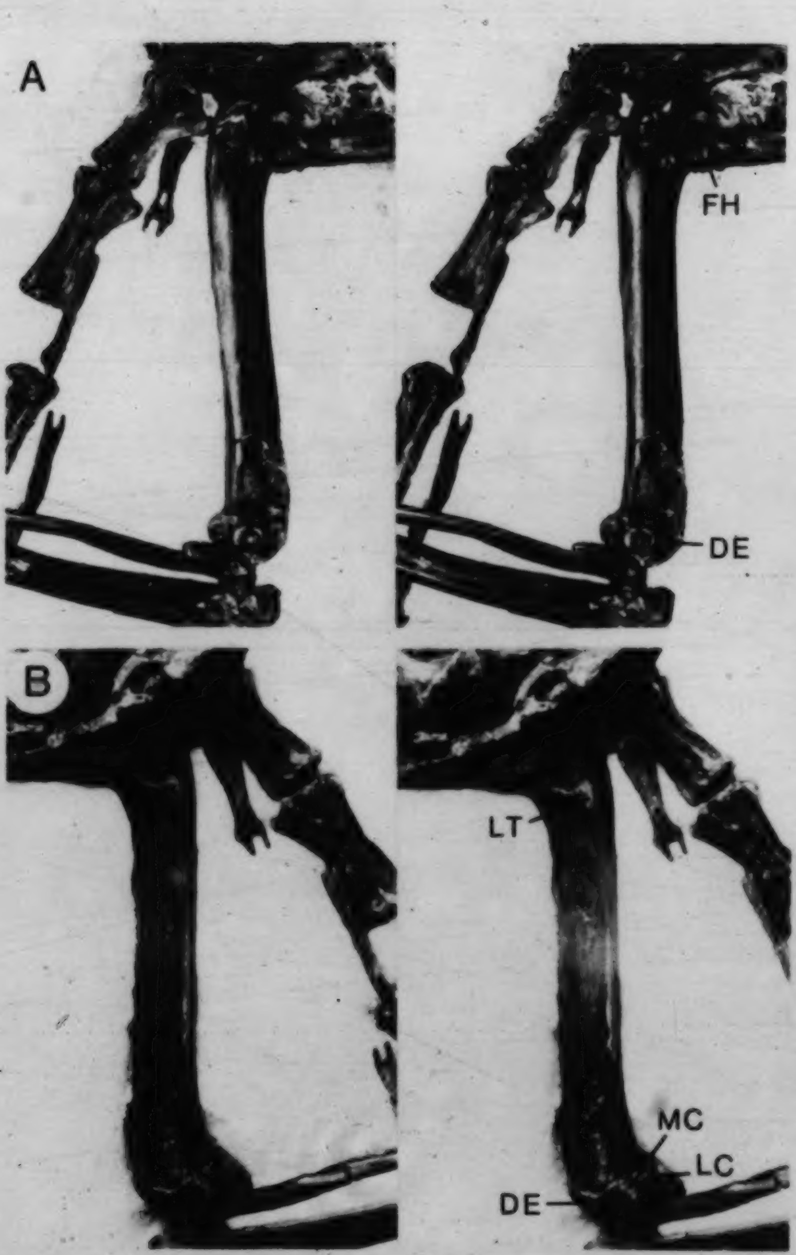
(i) Femur

UA 9001.- For descriptive purposes, the femur will be treated as if lying in a horizontal plane.

The geometrical shape of the femoral head, which is set off from the shaft by a well developed cylindrical neck, is greater than a hemisphere (Fig. 30). In either proximal or distal view, the femoral head is set obliquely to the shaft, rising dorsomedially.

The greater trochanter extends the long axis of the shaft proximally to a level slightly beyond that of the head. The proximal terminus is expanded and overhangs the main part of the greater trochanter dorsally, medially, and laterally. In side profile, the ventral margin of the

Figure 30. Ptilodus kummae, n. sp. (UA 9001), stereophotographic pairs: (A) lateral (about x2.1), and (B) medial (about x2.3) view of right femur. DE - distal epiphysis, FH - femoral head, LC - lateral condyle, LT - lesser tuberosity, MC - medial condyle.


A
FH
DE
B
LT
MC
LC
DE

greater trochanter is gently convex. A low crest passes distally along the ventral side of the shaft from the greater trochanter to slightly beyond mid-length. The digital fossa is not extensive but is narrow, deep, and elongate, and is situated in the apex of the V between the proximal terminus of the greater trochanter, the lesser trochanter, and the femoral head. The lesser trochanter projects ventrally and is simply a raised, rounded eminence, approximately one-third the size of the femoral head. A low, rounded ridge extends proximally from the lesser trochanter towards the femoral head; another extends towards the greater trochanter. A shallow longitudinal fossa is developed immediately lateral to the lesser trochanter. According to Simpson and Elftman (1928) this fossa may be the second part of a divided digital fossa.

The shaft is long, slender, and is round in cross section at mid-length but more elliptical proximally. A nutrient foramen is developed distal to the lesser trochanter about one-third of the way down the shaft.

The distal epiphysis of the femur was not completely fused to the diaphysis at the time of death and the position of the epiphyseal cartilage is still visible. The distal end presents three articular surfaces: a medial and a lateral condyle and a femoral trochlea, or patellar groove. The patellar groove is asymmetrical relative to the mid-line of the shaft, running obliquely proximomedial-distolaterally and terminating dorsal to the lateral condyle. The two condyles are directed ventrally and are separated by a broad, U-shaped notch, the intercondyloid fossa. The popliteal fossa proximal to the intercondyloid fossa is not deep. The condyles assume only a ventral position and are not extended onto the distal part of the distal epiphysis. The lateral condyle is transversely more expanded than the medial condyle; the lateral epicondyle is also larger than the medial one. The epicondyles are irregular in topography and are rugose. They provided proximal sites of attachment for the collateral ligaments of the femoro-crural joint. A shallow but distinct, round fossa, presumably the extensor fossa, which provided origin for *m. extensor digitorum longus*, is located anterodorsally between the lateral ridge of the patellar groove and the lateral epicondyle.

Other Material.- A *fovea capitis internus*, for attachment of the femoral head ligament, cannot be seen on UA 9001 owing to the head's tight articulation with the acetabulum. However, an isolated femoral fragment of *P. kummae* preserving the head and greater trochanter (UA 11301) exhibits a fairly large, flattened, slightly roughened area on the posterodorsomedial side of the femoral head (Fig. 29E). Suggestions of a similarly flattened area can be seen on femora of *Ptilodus montanus* (AMNH 35490), and, as identified by Deischl (1964), *Mesodma thompsoni* (UMVP 1423) and *Cimexomys minor* (UMVP 1421), as well as on several unidentified allotherian femora in UA collections from the

Hell Creek Formation. This area is fairly discrete and probably provided attachment for the ligamentum capitis femoris.

(j) Patella

UA 9001.- The patella is a small, elliptical bone that is preserved only on the right side and directly overlies the lateral condyle of the tibia (Figs. 31A, 32B). Although somewhat crushed, it appears to have been concave proximally and convex distally, as would be expected.

(k) Tibia

UA 9001.- The proximal surface is comprised of a small, ovoid medial condyle (see Fig. 31B), which is oriented anterolateral-posteromedially, and a much larger lateral condyle, which is covered by the patella and crushed on the right side (Fig. 31A, 32B) and wedged between the femoral and iliac bodies on the left (Fig. 32A). Although crushed and broken, it appears that the lateral facet was convex and extended posteroventrally. This extension graded into the prominent lateral flange described below but, in doing so, provided a large, flat facet on the posterior surface that articulated with the fibular head. The intercondyloid eminence is distinct and is higher posteriorly than

Figure 31. Ptilodus kummae, n. sp. (UA 9001), stereophotographic pairs: (A) lateral (about x2.1), and (B) medial (about x2.3) view, right tibia and fibula. DEF - distal epiphysis of fibula, DET distal epiphysis of tibia, LFF - lateral fibular flange, LTF - lateral tibial flange, MC - medial condyle, P - patella.

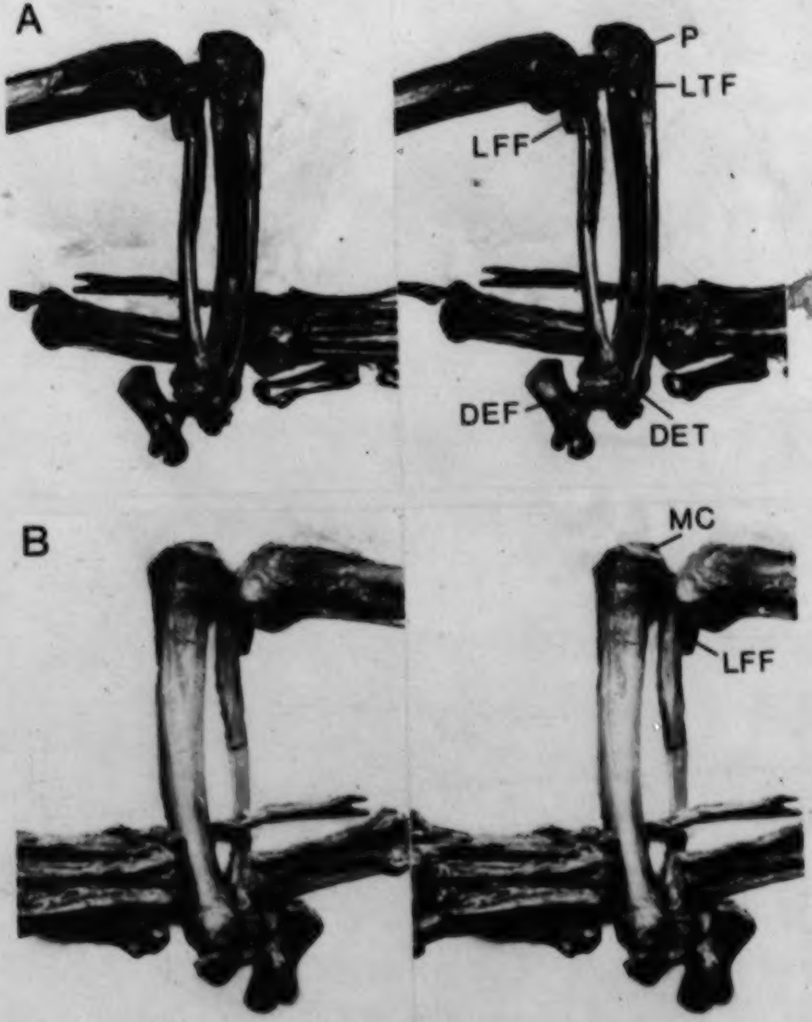
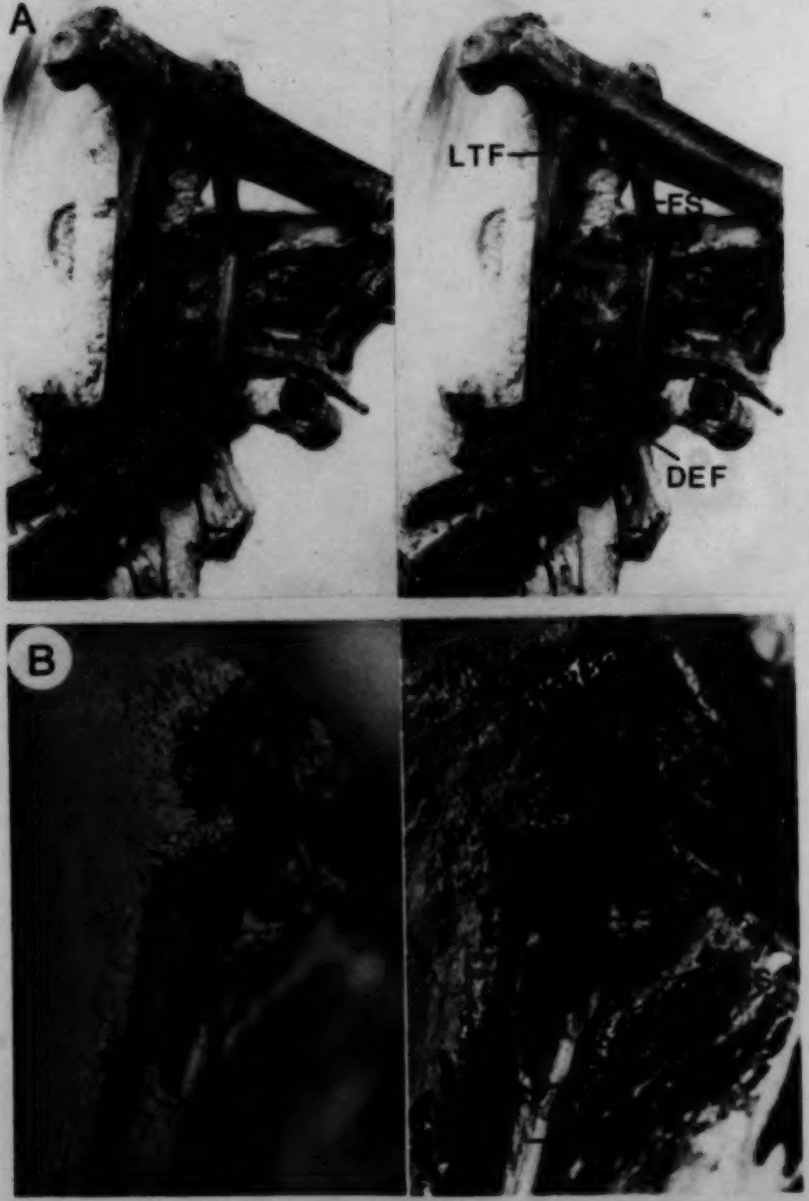

A
P
LTF
LFF
DEF
DET
B
MC
LFF

Figure 32. Ptilodus kummae, n. sp. (UA 9001), stereophotographic pairs: (A) anterior view (about x2.3) of left tibia and fibula, and (B) dorsolateral view (about x4.3) of right femoro-crural articulation. DEF - distal epiphysis of fibula, FE - femur, FT - facet for tibia, FS - fibular shaft, LTF - lateral tibial flange, P - patella.


A
LTF
FS
DEF
B

anteriorly. A large hook-like flange descends ventrolaterally from the posterolateral corner of the proximal terminus. A web of bone separates the protuberant flange from the shaft of the tibia and, anteriorly, forms a shallow fossa between the two structures.

The anterior surface of the tibia is evenly convex, there being no distinct tibial tuberosity developed proximally. Posteriorly, just below the proximal articular surface, the tibia is very deeply excavated.

At mid-shaft and distally, the shaft is, in cross section, convex anteriorly and rather flat posteriorly.

As on the femora and fibulae, the distal articular surface can still be differentiated from the shaft by a distinct epiphyseal line. A medial malleolus is but slightly developed. There are two facets on the distal articular surface; one is located on the lateral slope of the medial malleolus, the other occupies the lateral half of the distal surface and lies in a nearly horizontal plane. The two facets are closely conjoined but are separated by an oblique groove that accommodated the oblique ridge separating two corresponding facets on the astragalus.

Other Material.- The very deeply excavated posteroproximal surface of the tibial head appears to be consistently developed in allotherians. This fossa can be better seen on several specimens in UA collections from the

Hell Creek Formation (e.g. UA 11995, Fig. 33A). It is wide transversely, extends distally for approximately one-fourth the length of the shaft, and, in fact, undercuts the posterior half of the proximal articular surface. The result of the deep hollowing out is that, in cross section just below the proximal terminus, the shaft is lenticular, i.e., anteriorly convex and posteriorly concave.

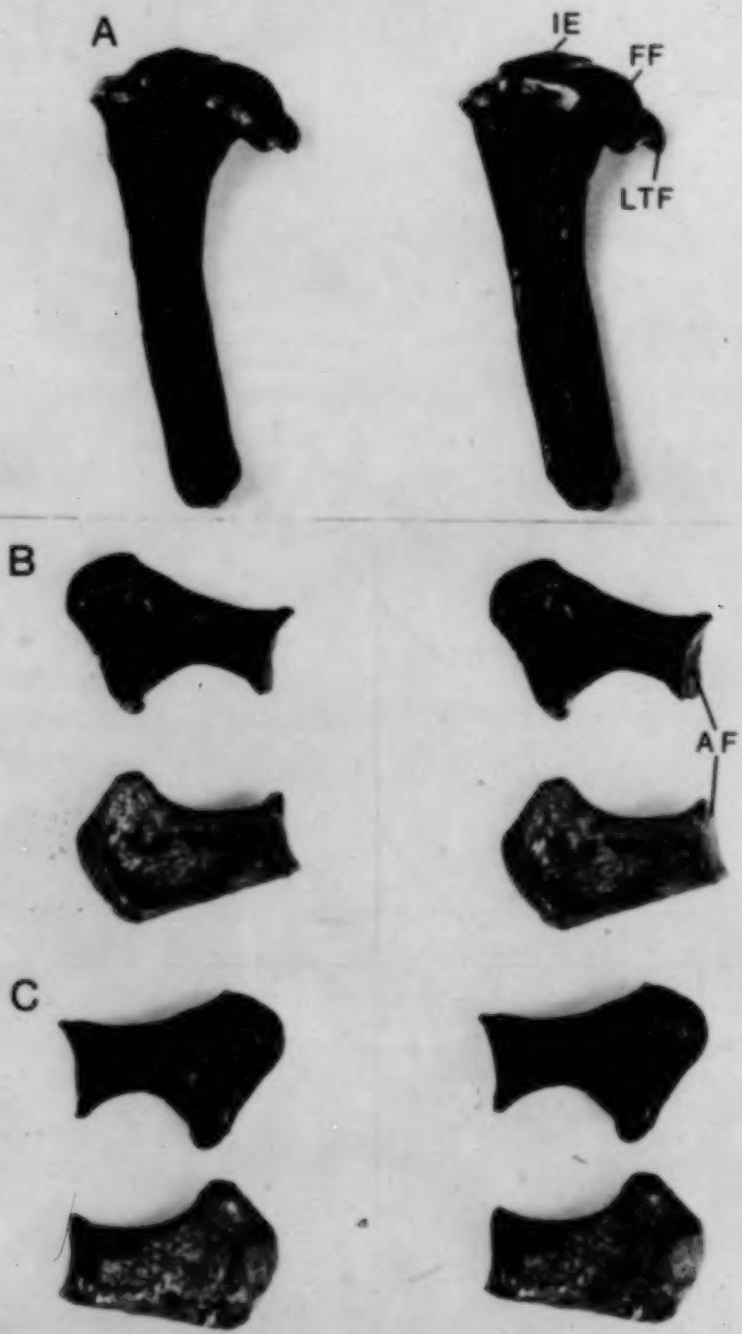
Also better seen on UA 11995 is the large, flat facet on the posterior surface of the tibial head for articulation with the fibula.

(1) Fibula

UA 9001.- The fibula is a very poorly known bone in multituberculates; its preservation in UA 9001 provides the first record of the complete bone (Figs. 31, 32). The orientation of the fibula, however, relative to the tibia, is not certain; the most parsimonious interpretation is given below.

It appears that, on the tibial head, the large flat facet that faced posteriorly and was situated on the lateral side of the posterior margin of the head articulated with a corresponding large, flat facet on the fibular head (Fig. 32B). If this interpretation is correct, the fibula was, at least proximally, situated posterior to the tibia but towards the lateral side of the tibial head. Distally,

Figure 33. Stereophotographic pairs: (A) posterior view of proximal fragment of right tibia (UA 11995), unidentified multituberculate, Hell Creek Formation, about x8.7; (B) side 1, and (C) side 2 of parafibulae? (top - UA 9001, Ptilodus kummae, n. sp.; and bottom - UA 11996, unidentified multituberculate, Hell Creek Formation), about x6.5. AF - articular facet, FF - facet for fibula, IE - intercondyloid eminence, LTF - lateral tibial flange.


A
IE
FF
LTF
B
AF
C

however, the fibula articulated directly lateral to the tibia.

The posterior surfaces of both the left and right fibular heads are slightly hidden by overlying bone. The posterior margin of the left fibular head, however, exhibits a large, convex facet that articulated with the parafibula. From its posterolateral corner, the fibular head is extended as an elongate, ventrolaterally directed, protuberant flange, which is very similar to that of the tibia but differs in being longer and more slender. Owing to the anteroposterior alignment of the proximal ends of the tibia and fibula the lateral flanges of those bones were also closely aligned in an anteroposterior relationship. Presumably, the flanges provided sites for musculotendinous attachment.

The shaft of the fibula is cylindrical, less robust than the tibial shaft, slightly bowed posterolaterally at mid-length, and expanded distally to accommodate the large distal epiphysis. The epiphyseal line can still be distinguished on the right fibula. The distal epiphysis of the left fibula is separated and displaced from the diaphysis. The distal surfaces of both epiphyses are hidden from view by overlying bone but it can be seen that the medial side presents a concave articular facet (for the ?lunula, see below), the lateral side presents a convex one, and a small projection is developed on the posterolateral corner.

(m) Parafibula?

UA 9001.- Two small bones, obviously a bilaterally symmetrical pair, are loosely associated with the hind limbs and are thought to be parafibulae (Fig. 33B, C). Each parafibula bears a small, elliptical, concave articular surface that distally gives rise to a short, constricted neck region, and, finally, to the distal end, which is flattened in one plane and expanded in the plane perpendicular to the first. Trial articulation with the large convex facet on the posterior surface of the proximal end of the fibula provided an exact fit and was the primary criterion used in identification of this bone. The bones are, however, exceedingly large for parafibulae.

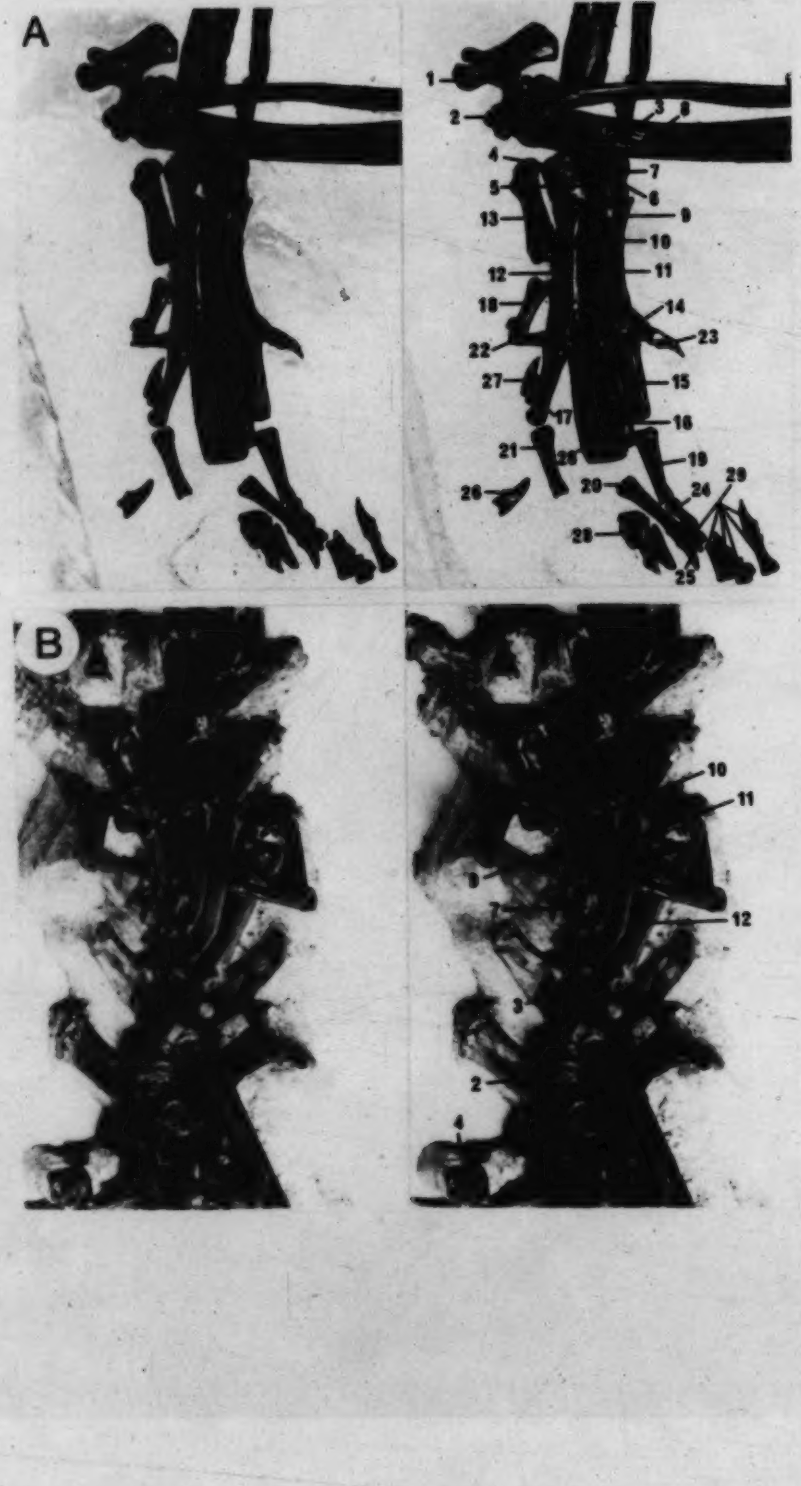
Other Material.- Only one other specimen of a multituberculate parafibula has been found. This specimen (UA 11996 - Fig. 33B, C) is from the Hell Creek Formation and pertains to a relatively large multituberculate. The bone is structurally very similar to the parafibulae of UA 9001.

(n) Tarsus

UA 9001.- The bones of the right tarsus are preserved in an almost articulated state (Figs. 34A, 35); those of the left tarsus are much more disarticulated and only the calcaneum, astragalus, cuboid, navicular, ecto- and entocuneiforms can be identified with confidence (Figs. 34B, 36).

The calcaneum is superficially of typically mammalian aspect (Fig. 36). The tuber calcanei is large, comprising the posterior half of the bone, and is laterally compressed. Its posterior terminus is dorsoventrally expanded and convex in lateral profile. Directed dorsally, the proximal facet for the astragalus (astragalocalcaneal facet) is large, strongly convex, tapered in transverse width distally, and is situated just medial to the mid-axial line of the tuber. A small, anteroposteriorly elongate eminence is developed just posterolateral to the astragalocalcaneal facet. A prominent and wide calcaneal sulcus separated the astragalocalcaneal facet from the sustentacular facet, which is directed medially and somewhat dorsally (approximately 50° to the astragalocalcaneal facet) and is flat and tear-drop shaped, its apex directed distally. An expansive, round, and convex area on the dorsolateral aspect of the distal end of the calcaneum provided for tendinous attachment. The roughened area also extends onto the plantar aspect of the calcaneum but narrows and terminates between

Figure 34. *Ptilodus kummae*, n. sp. (UA 9001), stereophotographic pairs: (A) dorsal view of right pes, about x2.1, and (B) ventral view of left pes, about x2.3. 1 - calcaneum, 2 - astragalus, 3 - navicular, 4 - cuboid, 5 - ectocuneiform, 6 - mesocuneiform, 7 - entocuneiform, 8 - tibiale, 9 - metatarsal I, 10 - metatarsal II, 11 - metatarsal III, 12 - metatarsal IV, 13 - metatarsal V, 14 - proximal phalanx I, 15 - proximal phalanx II, 16 - proximal phalanx III, 17 - proximal phalanx IV, 18 - proximal phalanx V, 19 - middle phalanx II, 20, middle phalanx III, 21 - middle phalanx IV, 22 - middle phalanx V, 23 - distal phalanx I, 24 - distal phalanx II, 25 - distal phalanx III, 26 - distal phalanx IV, 27 - distal phalanx V, 28 - vertebra, 29 - manual phalanges, 30 - lunula.


A
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16
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26
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25
B
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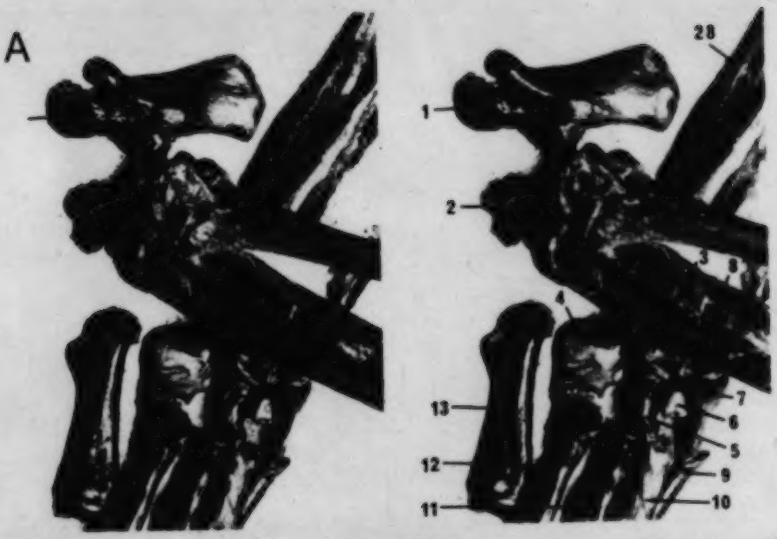
12
3
2
4

Figure 35. Ptilodus kummae, n. sp. (UA 9001), stereophotographic pairs: (A) dorsal, and (B) ventral view, right pes. Symbols as in Fig. 34. About x4.3.

A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B

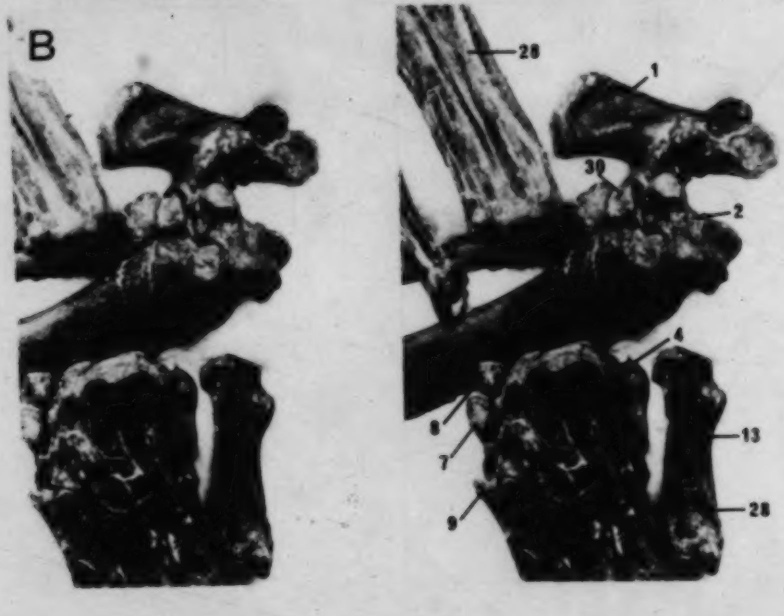
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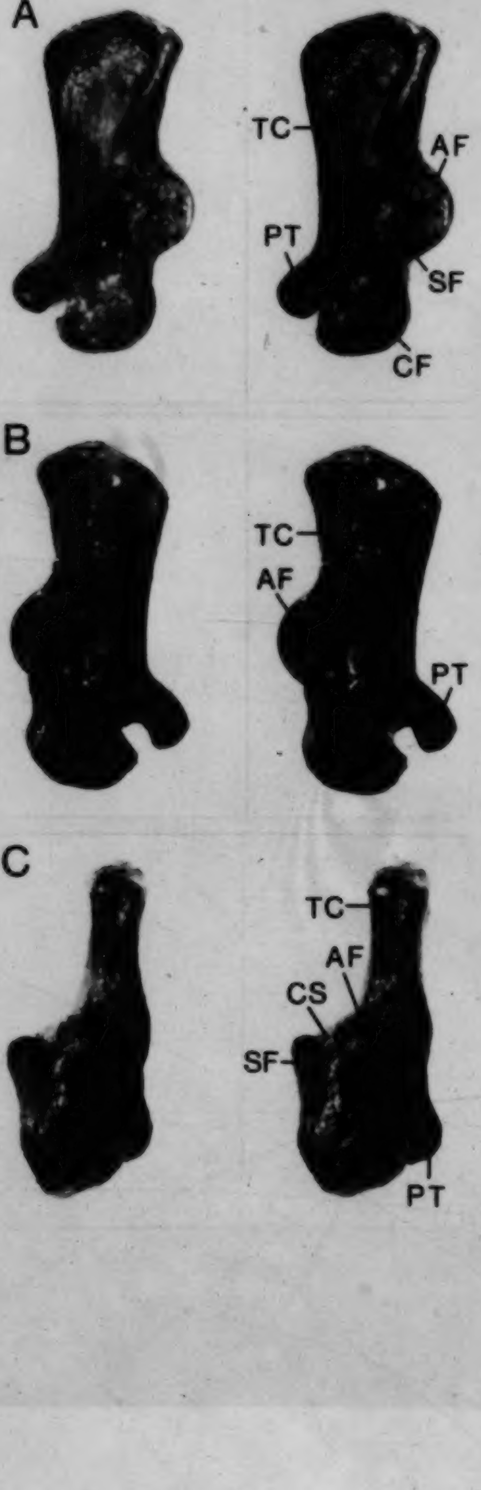
Figure 36. Ptilodus kummae, n. sp. (UA 9001), stereophotographic pairs: (A) medial, (B) lateral, and (C) dorsal view of left calcaneum. AF - astragalocalcaneal facet, CF - cuboid facet, CS - calcaneal sulcus, PT - peroneal tubercle, SF - sustentacular facet, TC - tuber calcanei. About x6.4.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TC
AF
CS
SF
PT

the cuboid facet and the deep groove separating a large distolateral process, the peroneal tubercle, from the calcaneal body. The cuboid facet is round, slightly concave, and faces anteroventromedially. The peroneal tubercle is very prominent and projects anteroventrolaterally. It bears an elongate, roughened area dorsally, which was probably structurally related to the round area (described above) developed distally on the calcaneal body. The tubercle is oval in cross section and terminates by swinging slightly dorsomedially.

The dorsal surfaces of both astragali of UA 9001 cannot be seen owing to overlying bone but, structurally, they probably do not differ considerably from that of *Eucosmodon* sp. (see Granger and Simpson, 1929, fig. 24B); other aspects of the astragalus appear very similar in the two genera.

The astragalus is dorsoventrally much thicker medially than laterally. The calcaneoastragalar facet, situated on the plantar aspect of the lateral side of the astragalus and facing ventrally, is almost circular in outline, with a marginal indentation medially, and is concave. The medial half of the plantar aspect is occupied by the astragalar sustentacular facet, which is directed ventrolaterally. The astragalar foramen pierces the astragalus midway along an imaginary line drawn between the posterior margin of the calcaneoastragalar and sustentacular facets. A canal, formed by the calcaneal sulcus and the plantar surface of the astragalus, is developed as an anterolateral continuation of the astragalar foramen. In pelycosaurs, an homologous passage is presumed to have allowed passage of an artery or vein, whereas in mammals it is occupied by an interosseus ligament, which stabilizes the sub-talar joint (Jenkins, 1971a). The astragalus is expanded posteriorly behind the astragalar foramen. The convex naviculoastragalar facet on the prominent astragalar head follows an oblique path, passing, from its lateral border midway along the anterior surface, ventromedially and then posteroventrally. In perpendicular section to the longitudinal axis of the facet, the facet is concave, thus forming a saddle-shaped articulation with the navicular.

The navicular is an elongate bone, which, along its longitudinal axis, is concave proximally and convex distally. Through manipulation of the right pes of Eucosmodon sp. (AMNH 16325) the navicular was determined to have lain in an oblique plane, being oriented dorsolateral-ventromedially. The right pes of UA 9001 preserves the navicular in a similar orientation. The facet for the astragalus is concave. Although the distal surface is generally convex there are two facets contained within it; one is concave and articulated directly anteriorly with the ectocuneiform; the other appears flatter and articulated with the mesocuneiform distomedially. Contact with a dorsoventrally concave facet on the cuboid distolaterally was also present.

The shape of the cuboid is tabular, the lateral profile being almost square. Only the distal and medial cuboidal facets, of which there are four, are clearly preserved in UA 9001 and are as follows: 1) a small, round facet for the ectocuneiform developed dorsally on the medial face; 2) a shallowly concave facet for the navicular on the proximomedial face; 3) a concave, vertically elongate facet for metatarsal IV present distally; and 4) a rather flat facet for metatarsal V distolaterally. Although not wholly visible, the facet for the calcaneum was large, slightly concave, and developed dorsally on the proximolateral corner of the cuboid.

The ectocuneiform is also tabular and oriented vertically. Both its distal and proximal articulations, with metatarsal III and the navicular, respectively, are dorsoventrally concave. Proximodorsally, on its medial surface, the ectocuneiform contacts the mesocuneiform via an oval facet, oriented proximodorsal-distoventrally. Along the proximal third of the lateral surface an elongate facet maintained contact with a corresponding facet on the cuboid.

Only the dorsal aspect of the mesocuneiform, which is rectangular in outline, can be seen. It is anteroposteriorly shorter than the ectocuneiform and articulated with the navicular proximally, the entocuneiform medially, via a slightly concave distal facet with metatarsal II, and with the ectocuneiform laterally.

The entocuneiform is the longest of the three cuneiform bones. It is laterally compressed and bears a strongly concave facet distally and a shallowly concave facet proximally. The ventral projection of the distal facet is more slender and less transverse than the dorsal projection. The distal facet formed an interlocking saddle-shaped articulation with metatarsal I. In the reconstructed pes of Eucosmodon sp. provided by Granger and Simpson (1929, fig. 23) the narrow ventral lip of the entocuneiform is dorsal rather than plantar in position. Trial articulations with the hallucal metatarsal of Eucosmodon sp., according to Granger and Simpson's orientation of the entocuneiform, restrict the digit to an awkward, nearly perpendicular position. Further, the metatarsals of the right pes of UA 9001 are preserved in tight articulation with one another, at least medially, and the narrow lip on the entocuneiform is clearly in a ventral position.

Preserved with the more or less intact right tarsus of UA 9001 are two rather problematical small bones. The first (Figs. 34A, 35A) almost certainly articulated via a convex facet with the proximal terminus of the entocuneiform. Its other articulations are less clear but contact with the navicular laterally is highly probable and perhaps also with the astragalus proximally. The position of the bone would indicate that it is probably the tibiale, or tibiale navicular, the homologies of which have recently been discussed by Lewis (1964). Lewis reviewed the occurrences of the tibiale among mammals, namely, in the Monotremata, Rodentia, Galeopithecus, Hyrax, Dinocerata, and certain fossil ungulates. In monotremes the tibiale articulates proximally and laterally with the astragalus and distally with the navicular. The oblique orientation of the navicular in UA 9001 provides space for the tibiale to articulate with the entocuneiform. The entocuneiform of known Allotheria probably did not, therefore, articulate with the navicular, contrary to the statement by Granger and Simpson (1929).

The second bone of dubious homologies is preserved in tight articulation with the distal articular surface of the fibula (see Fig. 30B). It is without doubt, neither the astragalus nor the calcaneum and it is probably not a sesamoid bone, as evidenced by its tight articulation with the distal end of the fibula. Only the medial surface of the bone can be seen; it is oval in outline and quite small. If the tentative orientation of the fibula is correct, the small bone articulated on the medial side of the distal terminus of the fibula. More than two tarsalia in the proximal row are, however, unknown among mammals. Early workers (see review by Lewis, 1964) reported the occurrence of a third proximal bone (the intermedium tarsi) in pedes of several marsupials, as well as in humans (named the os trigonum in humans but thought to represent the intermedium tarsi). Lewis (1964) concluded, however, (p. 207) "that the so-called marsupial intermedium is merely a lunula within an intra-articular meniscus" and that (p. 203) "there is ... little reason for regarding the anomalous human os trigonum as an intermedium tarsi. Perhaps it is not even the homologue of the marsupial lunula, and nothing more than an aberrant ossification of no morphological significance." Although the evidence is unclear, the miscellaneous proximal tarsal bone of P. kummae is here also considered to be a lunula, but discoveries of other non-therian articulated pedes may subvert this conclusion. If the bone is a true tarsal, its position is irreconcilable with presently accepted interpretations of homologies of individual mammalian tarsalia.

(o) Metatarsus

UA 9001.- The lengths of the metatarsals, in decreasing order, are III, IV, II, V, and I (see Fig. 34).

The proximal articular area of metatarsal I is dorsoventrally convex and articulated with the dorsoventrally concave saddle articulation of the entocuneiform. The distally directed ventral lip of the entocuneiform is wedged between two posteroventrally directed processes of the hallucal metatarsal, the medial one of which is much the larger. The shaft of metatarsal I, as in all the metatarsals, is elliptical, being dorsoventrally compressed. The distal articular surface cannot be seen.

Metatarsals II to IV are basically similar except in length and in the shape of the proximal bases, which become progressively wider from II to IV. Metatarsal V bears a prominent, rounded lateral projection just distal to the proximal facet. A similar process is developed in the cynodont described by Jenkins (1971a, p. 196), which is "similar to that in many mammals where short flexor and peroneal musculature may have inserted." The proximal articular surfaces of metatarsals II to IV are dorsoventrally convex. That of metatarsal V is limited to a small, dorsoventrally elongate, flat facet on the proximomedial corner of the bone.

An oblique groove between the apposed medial side of metatarsal III and the lateral side of metatarsal II, just distal to the proximal bases, probably provided passage for the perforating metatarsal artery from the dorsal to the plantar aspect of the hind foot.

Two oval plantar sesamoids are associated with the distal ends of metatarsals IV (left pes) and V (right pes), whereas a conjoined one is present on metatarsal II (left pes).

(p) Pedal Phalanges

UA 9001.- Pedal phalanges of all ten digits have been preserved in UA 9001 (Fig. 34).

The proximal and middle phalanges of the digits are all very similar, except in length (see Table 25), and are of typically mammalian conformation. The proximal articular surface of each is expanded and concave; the distal articulation is also expanded but is dorsoventrally convex. The distal articular ends of the proximal phalanges (except I) are transversely slightly convex but those of the middle phalanges and proximal phalanx I have a prominent trochlea developed to accommodate the distal phalanges. The shaft of each proximal and distal phalanx tapers distally and is elliptical in cross section. Several plantar sesamoids are loosely distributed throughout the phalanges of both pedes.

Distal phalanges of the pes are similar in structure to those of the manus but are considerably more elongate.

Table 25

Ptilodus kummae, n. sp., Pedal Measurements

	Digit I	II	III	IV	V
Metarsal length	6.9*	10.4	11.8	11.2	7.8
Proximal phalanx length	---	6.4	6.2	6.3	4.5
Middle phalanx length	---	5.7	5.7	5.5	3.8
Distal phalanx length	3.3	3.6	3.4	3.5	3.3

*approximate

D) Postcranial Adaptations of *Ptilodus kummae* and Other Multituberculates

(i) Axial Skeleton

Ankel (1967, 1972), following the work of Rockwell *et al*. (1938) on human vertebrae, has determined that three different orientations of the zygapophyses occur in the presacral region of primates. The surfaces of the zygapophyseal joints are arranged relative to the sagittal plane such that, in end view, they lie on a circular arc, the center of which occurs on the sagittal plane. In the cervical series, the center of the zygapophyseal circle lies dorsal and external to the vertebrae; in the lumbar series, the center of the circle also lies dorsally but the circumference is much smaller. In the thoracic series, by contrast, the center lies ventral to the zygapophyses and within the centrum (see Ankel, 1967, fig. 6) and, consequently, allows more torsional movement than in either the cervical or lumbar regions. Torsion in the thoracic series, however, is primarily restricted by the presence of ribs (Ankel, 1967).

In *P*. *kummae* at least the last twelve presacral vertebrae, including five thoracics (here defined by the presence of demifacets for the ribs and not by a different orientation of the zygapophyses), exhibit a zygapophyseal circle whose center is dorsal to the neural arch. The same holds true for the thoracic vertebrae of *Eozostrodon*, as is apparent from the figures of Jenkins and Parrington (1976), and, incidentally, in *Plesiadapis* as well (Simpson, 1935b; Szalay *et al*., 1975). Presumably, therefore, torsional movements in the thorax of these mammals is restricted not only by the ribs but also by the orientation of the zygapophyses. Furthermore, the degree of thoracolumbar differentiation in *P. kummae* and *Eozostrodon* appears to be intermediate in development between cynodonts and more advanced mammals.

Unfortunately, the articular ends of most of the presacral vertebrae are not visible because of deformation, the presence of overlying bone, or close apposition of contiguous vertebrae, and the region of maximum mobility cannot be determined. That the column was capable of considerable flexion and extension is, however, indicated by the following features: 1) the transversely broad and dorsoventrally depressed centra (Hatt, 1932); 2) the far anterior position of the anticlinal vertebra (Slijper, 1946); and 3) the shape of the articular ends of centra posteriorly in the thoracic series. The anterior end of each centrum is, in side view, obliquely anterodorsal-posteroventral in orientation; the posterior end is flat. The intervertebral wedge that results probably permitted some flexion in this region. Extreme extension, however, at least in the posterior thoracic and lumbar regions, would have been prevented by the low, anterodorsal inclination of the spinous processes, which, on extension, would have abutted the neural arch, between the postzygapophyses, of the preceding vertebra. The tongue-in-groove relationship of the spinous process of one vertebra between the postzygapophyses of the next most anterior vertebra also disallowed lateral undulatory movements of the trunk.

The caudal vertebrae of UA 9001 represent the most complete tail known for a multituberculate and indicate that, in P. kummae, the tail was large and extremely long, as earlier suggested from more incomplete material by Gidley (1909). Cope has variously described the tail of Taeniolabis as "large" (1882b, 1884b) or "stout" (1884a). That of Eucosmodon sp. is portrayed as having been "long and heavy" (Granger and Simpson, 1929). The length and number of vertebrae reconstructed in the tail of Mesodma thompsoni by Deischl and Sloan (in Sloan and Van Valen, 1965, fig. 3) may have been underestimated and is probably further incorrect in that the elongate caudal vertebrae of known allotherians are not immediately posterior to the sacrum, as illustrated, but, rather, are preceded by a series of short, robust vertebrae that bear well-developed processes.

Relatively short centra in the anterior caudal region, as exhibited by both P. kummae and Eucosmodon sp., indicate a propensity for dorsal flexion of the tail, as, for example, in rabbits and squirrels. By contrast, almost all ricochetors do not dorsally flex the tail and show little or no abbreviation of proximal caudal centra (Hatt, 1932).

Unfortunately, there appears little that would osteologically differentiate prehensile from non-prehensile tails (Haines, 1958), although Matthew (1904) has suggested that the tails of all primitive Tertiary mammals were probably prehensile. This hypothesis remains to be adequately tested. It may be pertinent to note, however, that the large size and persistence of the haemal arches, which allowed passage of the median caudal artery and vein, into the terminal caudal vertebrae of UA 9001 suggest a relatively highly vascularized and, therefore, probably a muscular tail. Furthermore, the nerve supply to the tail appears to have been considerable, as indicated by the presence of a rudimentary neural arch as far posterior as Cd 7. However, unlike prehensile-tailed anthropoids (Ankel, 1961, 1962), the terminal caudal vertebrae are not dorsoventrally flattened or abbreviated in length.

(ii) Pectoral Girdle

No bones resembling an interclavicle or clavicle were found in UA 9001. An interclavicle has, however, been tentatively ascribed to a multituberculate by McKenna (1961) and both interclavicles and clavicles are reported to occur in the triconodont Eozostrodon (Jenkins and Parrington, 1976). Conclusive evidence, that is, association in complete or partial skeletons, to indicate that these bones are present in either multituberculates or triconodonts is still lacking. The prominent and posteriorly directed acromion on the allotherian scapulocoracoid (UA 11992) from the Hell Creek Formation (see Fig. 18) cannot be taken as evidence for the presence of a clavicle. Several normally aclaviculate Recent mammals possess a well developed acromion (Jenkins, 1974a). However, other structural features of the postcranium indicate that P. kummae possessed a generalized quadrupedal stance similar to most therians in which "the weight-bearing forefoot is commonly placed lateral to a sagittal plane through the shoulder joint ... In this position ... the clavicle ... prevents medial displacement of the shoulder" (Jenkins, 1974a, p. 81).

The orientation of the glenoid fossa of the scapulocoracoid in multituberculates (see McKenna, 1961, figs. 1-3) is basically the same as that of therians, in which it faces primarily ventrally, rather than posterolaterally and only slightly ventrally as in cynodonts (Jenkins, 1970, 1971a). The orientation of the glenoid in monotremes can be related to fossorial habits (Jenkins, 1970, 1971a) and a comparison, therefore, would not be particularly instructive. The contribution of the coracoid to the anterior part of the glenoid cavity adds considerably to the craniocaudal curvature of this structure, thereby permitting further retraction of the humerus than would otherwise be possible, preventing dislocation of the humeral head from the glenoid fossa during flexion, and necessitating a relatively small amount of scapular rotation. Some therian mammals develop an analogous articular facet by the anteroventral elongation of the glenoid fossa of the scapula, rather than by contribution from the coracoid (Roberts, 1974). However, dislocation of the shoulder joint is prevented in therians lacking such an anteroventral lip by rotation of the scapular blade forward on the thorax (Roberts, *ibid*.; Eaton, 1944; Maynard-Smith and Savage, 1956), an action that perhaps was unnecessary in multituberculates.

The contribution of the coracoid to the shoulder joint is a prototherian and reptilian feature, and is not the condition generally shown by adult therians (Romer, 1922; McKenna, 1961; Crompton and Jenkins, 1973). The scapulocoracoid of *Eozostrodon*, for instance, shows a large contribution of the coracoid to the glenoid articulation; however, as in monotremes, the large procoracoid, although retaining contact with the scapula, is excluded from the glenoid facet (Kermack and Mussett, 1959; Jenkins and Parrington, 1976). In both pelycosaurs and cynodonts the procoracoid contributes to the glenoid fossa but, in cynodonts, it is considerably reduced (Jenkins, 1971a). The procoracoid, as inferred by McKenna (1961), appears to have been absent in multituberculates, at least in species for which the scapulocoracoid is known.

The pattern of musculature attendant to the allotherian pectoral girdle has been outlined by McKenna (1961) and Jouffroy and Lessertisseur (1967).

(iii) Forelimb

It is obvious, both from the shape of the glenoid fossa on the scapulocoracoid and from the evenly rounded head of the humerus, that the glenohumeral articulation did not restrict humeral positions as it did in pelycosaurs (Jenkins, 1971a). More detailed inferences concerning the structural organization and function of the shoulder joint must await descriptions of the Mongolian specimens (Kielan-Jaworowska, in prep.). Present knowledge of the anatomy of the proximal end of the humerus in allotherians is restricted to fragments from _P. montanus_ (USNM 6076) and _P. kummae_ (UA 9001) and a relatively complete humeral head of _Djadochtatherium matthewi_ (AMNH 20440). The humerus of

AMNH 20440, however, was not seen for this study and Simpson's (1928c) figures are not adequate for precise functional interpretations. The presumed proximal portion of a humerus of Mesodma thompsoni (UMVP 1402) has been described and figured by Deischl (1964) and provided the basis for the reconstructed humerus in fig. 3 of Sloan and Van Valen (1965). UMVP 1402, however, is the distal fragment of an anuran humerus.

The distal articular surface of the multituberculate humerus is comprised of a lateral radial condyle and a medial ulnar condyle, separated by an intercondylar groove (Jenkins, 1973), as in other known non-therian humeri (Jenkins, ibid.; Jenkins and Parrington, 1976). This condylar pattern of humero-ulnar articulation differs basically from the trochlear pattern of therians (Jenkins, 1973; also early recognized as being different by Broom, 1910) and, therefore, has certain functional implications.

During its propulsive phase the humerus of non-cursorial living mammals (Jenkins, 1971b), and, probably in at least some Jurassic mammals from the Morrison Formation (Jenkins, 1973), is oriented obliquely to the sagittal plane and adducts, elevates, and rotates medially. The anatomical similarity between the distal ends of humeri of the Jurassic mammals and P. kummae suggests that a similar type of excursion was present in the latter. The restricting surfaces of the ulnar condyle on the humerus and the apposing articular area on the ulna prevent any orientation of the ulna other than in a nearly sagittal plane, that is, "the forearm remains parallel to the direction of locomotion despite complex humeral movement" (Jenkins, *ibid*., p. 288). Furthermore, as Jenkins has suggested for Jurassic mammals, the oblique orientation of the facet for the ulnar condyle probably maintained the ulnar shaft in a sagittal plane during the propulsive phase.

Relative to other observed allotherian humeri, the perforate olecranon fossae on the humeri of *P. kummae* and *P. montanus* imply that the humero-ulnar articulation in these species permitted a greater degree of extension of the antebrachium.

The extensive development of the articular circumference of the radial head, in addition to the circular dorsal outline of the radial head (that part that articulates with the radial notch of the ulna), a slightly concave radial notch on the ulna, and the free and more or less evenly developed radius and ulna are features associated with maximal amounts of pronation and supination of the manus. The capacity for pronation and supination in *P. kummae* appears to be considerably greater than the condition previously estimated for known Jurassic (Jenkins, 1973) and Triassic (Jenkins and Parrington, 1976) mammals. As in *Eozostrodon* (see Jenkins and Parrington, 1976), however, the capitular depression on the radial head of *P.*

kummae is oval and set obliquely to the long axis of the shaft. This feature presumably limited the antebrachium to only moderate amounts of pronation and supination.

Functional considerations of the carpal anatomy of *P. kummae* are perhaps somewhat premature owing to the tentative identification of the individual bones as well as of their articular relationships. Furthermore, as Yalden (1970, p. 482) points out, "All the muscles which affect movements at the wrist insert distally to it, either to the metacarpal bones or into the phalanges ... Hence the precise form of movement between the carpal bones depends very largely on the shapes of the surfaces of these bones." Few of the articular facets can be seen or clearly discerned on the carpus of UA 9001; however, the general shapes of the carpal bones preserved on the medial side of the manus may be indicative of the positions of the moveable joints.

"The possible movements of the wrist in mammals can be resolved into three components: flexion-extension, or hingeing in the sagittal plane; ulnar or radial deviation, hingeing in the transverse plane; and axial rotation, supination-pronation" (Yalden, 1972, p. 383). The amount of radial (medial) or ulnar (lateral) deviation cannot be meaningfully ascertained without the lateral portion of the carpus. Furthermore, the function of the carpus during supination-pronation has not been adequately determined, even for living mammals (Yalden, 1972), but, in any case, the carpus contributed a minor role relative to movements of the forearm. The capacity for flexion and extension of the carpus, however, appears to have been considerable in *P. kummae*. In flexor-extensor section (*sensu* Yalden), for instance, the strongly convex proximal surface of metacarpal III articulated with an equally strongly concave facet on the distal surface of the magnum. An almost identical reciprocally concavo-convex articular relationship is maintained between the magnum and the centrale and, possibly, between the centrale and the cuneiform and semilunar. The retention of the centrale in the carpus has provided for a double mid-carpal joint in this position. The articular relationships between the more medial carpal and metacarpal bones are less clearly visible. The articulation between the trapezoid and metacarpal II, however, is also concavo-convex but appears to be slightly less so than between the magnum and metacarpal III.

The presence of a prepollical carpal in the manus of *P. kummae* is not surprising. As determined by Bardeleben (1894), the prepollex is a normal component in mammalian pentadactyl forefeet, but in few is it as well developed as in *Ailuropoda* (see Davis, 1964). In *Ailuropoda* and other mammals the prepollex is associated with muscles (*Mm. abductor pollicus longus*, *abductor pollicus brevis*, *opponens pollicus*, and *palmaris longus*) that, in the absence of a prepollex, normally insert onto the base of the thumb (Davis, *ibid*.; Lessertisseur and Saban, 1967). In any case, the presence of a prepollex and its attendant musculature implies a functional "sixth digit" that probably acted in concert with the pollex and considerably enhanced the grip of the hand in *P. kummae*.

Unfortunately, an evaluation of the mobility of the pollex is severely limited by the inability to see the entire distal articular surface of the trapezium. In any case, however, the carpo-metacarpal joint is not of the "saddle" type (Napier, 1961) and, as such, the thumb was not capable of axial rotation and, therefore, was not opposable. Furthermore, the articular facet on the base of metacarpal I is dorsoventrally short but transversely elongate, suggesting that the amount of axial rotation and abduction-adduction was considerably restricted. A flat intermetacarpal articulation between the bases of metacarpals I and II further limited the capacity for abduction and, especially, adduction of the pollex. The amount of digital convergence and, hence, prehensility (assessed from the relative depth of the transverse carpal arch (Napier, 1961)) of the hand of *P. kummae* cannot be determined without the lateral carpals.

(iv) Pelvic Girdle

The significance of the dorsally-open acetabulum of the pelvis is unclear. Van Valen and Sloan (1966, p. 276) state that this condition "suggests a near or complete lack of ricochetal or gliding habits among multituberculates and may have permitted at most only a low possibility of arboreal activity." Elftman (1929), however, had earlier determined, in a functional analysis of marsupial pelves, that a dorsally incomplete acetabulum, as in Pseudocheirus, is indeed correlated with an arboreal habit, allowing greater freedom of movement of the femoral head. Gliding phalangers have an even less complete dorsal rim, allowing the femur to be abducted during the animal's glide. Furthermore, the femur, at least in Eucosmodon sp. and P. kummae was oriented in a nearly horizontal plane in the normal standing position (Simpson and Elftman, 1928) and perhaps exerted little dorsomedially directed stress on the acetabulum. Similar emargination of the superior rim of the acetabulum has been found in the Triassic triconodonts Eozostrodon, Megazostrodon, and Erythrotherium (Jenkins and Parrington, 1976) and the tritylodontid Oligokyphus (Kuhne, 1956). Jenkins and Parrington (1976) suggest that fibrocartilage may have filled in the dorsal border of the acetabulum in all these cases.

(v) Hind Limb

Jenkins (1971a) has lucidly analyzed femoral positions in pelycosaurs, cynodonts, and "non-specialized" mammals. Through this phylogenetic sequence of tetrapods, the distal end of the femur is progressively oriented further ventrally and medially with concomittant changes occurring at both proximal and distal articular ends. The ventrally directed medial and lateral distal condyles on the femur of UA 9001 suggest, however, that the femur of *P. kummae* was normally held in a nearly horizontal plane. If the rather flat *fovea capitis femoris* is correctly identified on UA 11301, an isolated right femoral fragment of *P. kummae*, further inferences can be made concerning femoral position inasmuch as, to paraphrase Jenkins and Parrington (1976), the *fovea* and its ligament move within the acetabular fossa, the deepest and central part of the acetabulum. If this is granted, the femur was normally positioned at about a 30° to 40° angle to the sagittal plane (a more accurate estimate would require disarticulation of the pelvis and femora of UA 9001). Further confirmation of this orientation is provided by the dorsomedial projection of the femoral head from the shaft, which, in generalized non-cursorial mammals "is apparently correlated with a femoral posture in which there is a relatively large angle (approximately 25° or more) between the femoral and body axes" (Jenkins, 1971a, p. 178). A similar normal standing posture has been determined for *Eucosmodon* sp. by Simpson and Elftman (1928).

The acetabular-femoral articulation shows unusual freedom of mobility of the femur in that the acetabulum is relatively open, especially dorsally, and the femoral head consists of greater than a hemisphere, typical of scansorial but not of cursorial, fossorial, or volant mammals (Hildebrand, 1974).

The knee joint of *P. kummae*, although the contained articular relationships are still far from clear, appears to represent an enhancement of conditions seen in *Eozostrodon*, *Megazostrodon*, and *Erythrotherium*. In *Eozostrodon*, for instance, Jenkins and Parrington (1976) have shown that the femur is also large and expanded distally, the medial condyle being narrower than the lateral, the corresponding medial condyle of the tibia is also narrower than the lateral, and is concave rather than convex, and a prominent laterally-projecting tibial flange is present (although much less developed than in *P. kummae*). Jenkins and Parrington (*ibid*.) have suggested that similar conditions (with the exception of the tibial flange) exist in generalized, non-cursorial therians such as *Tupaia* and *Didelphis*, in which some rotation at the knee joint is effected during the propulsive, weight-bearing phase of locomotion.

The fibula appears slightly shorter than the tibia and probably did not retain contact with the femur as it does in monotremes (Haines, 1942), most marsupials (Barnett and Napier, 1953b), and at least some Triassic triconodonts (Jenkins and Parrington, 1976). The functional significance of the peculiar articular relationships of the proximal head of the fibula of *P. kummae* is unclear but, in any case, according to the terminology of Barnett and Napier (1953a), the fibula of P. kummae was a mobile one, in that it is not anywhere fused to the tibia. Mobile fibulae in eutherians are "virtually limited to cats and bears among the Carnivora and to the majority of Primates ... All these animals are either remarkably well adapted to progression, often at high speeds, over rocky and uneven surfaces ... or are wholly or partly arboreal" (Barnett and Napier, ibid., p. 17). Extrapolation of the above statement to P. kummae, however, must await the determination of the type of tibio-fibular articulation, as it appears to be quite unlike that of any living mammal.

The horizontal and flat articulation between the tibia and astragalus of P. kummae and Eucosmodon sp. clearly indicates that the foot was plantigrade. Plantar contact of the calcaneum with the substrate provided extrinsic stability for the tarsus and thus for flexion and extension at the cruro-pedal joint. This stage had already been attained by therapsids (Jenkins, 1971a) except that both the calcaneum and astragalus were in contact with the substrate. The relatively flat proximal surface of the astragalus in multituberculates indicates that a rather limited degree of flexion and extension, relative to most therians, was possible at the cruro-pedal joint. In therians, a proximal trochlea, the sides of which articulate with the medial and lateral malleoli, is developed on the astragalus and thus permits a great degree of mobility. The presence of malleoli in therians stabilizes the cruro-pedal joint (Jenkins, 1971a). Malleoli are absent in cynodonts (Jenkins, ibid.), possibly in the Triassic triconodonts as well (Jenkins and Parrington, 1976) but are at least incipiently developed in *P. kummae*.

The presence of a small, elongate eminence just posterolateral to the astragalocalcaneal facet on the calcaneum may indicate some additional cruro-pedal articulation other than that between the astragalus and crus. If this eminence is an articular facet, it presumably would have contacted the osseus lunula, which is developed distal to the fibula, described above. A facet for fibular articulation is present in the same position in cynodont calcanei (Jenkins, 1971a, fig. 62B).

The calcaneoastragalar, or sub-talar, articulation of *P. kummae* and *Eucosmodon* sp. is very similar to that of cynodonts (Jenkins, ibid., p. 199) in which it "is a shallow ball and socket joint with the possibility of more than the inversion-eversion movements that characterize this joint in mammals." The astragalus, with its two plantar facets separated by an astragalar sulcus, was partially superposed on the dorsomedial surface of the calcaneum. As Jenkins has pointed out for cynodont astragali, however, the two facets are part of the same arc and therefore permitted axial rotation about the joint, and consequently, inversion-eversion of the pes. The presence of a strong transverse tarsal arch precluded the astragalus from plantar contact.

A distinct astragalar head for articulation with the navicular, a condition that apparently appears for the first time in Triassic triconodonts (Jenkins and Parrington, 1976), is also developed in *P. kummae* and *Eucosmodon* sp..

A transverse tarsal arch is prominently developed in both *P. kummae* and *Eucosmodon* sp. In *P. kummae*, only the distal articular surfaces of the cuboid, and of the ecto- and entocuneiforms can be observed. All three bones are transversely wider dorsally than ventrally, thereby producing what Jenkins (1971a) terms a "keystone" arch. The mesocuneiform of *Eucosmodon* sp. is almost rectangular in distal view but the cuboid, ecto- and entocuneiforms are shaped much as in *P. kummae*. Furthermore, the nature of the calcaneocuboid articulation produces a plantar angle between the two bones that is much less than 180°, therefore further increasing the height of the transverse arch.

The pedal phalanges of both *P. kummae* and *Eucosmodon* sp. retain the basic pattern seen in the Triassic triconodonts, which Jenkins and Parrington (1976) conclude were capable of pedal prehension. Osteological features in *P. kummae* correlated with good prehensile capabilities include elongate, transversely compressed claws, well-developed trochleae at the distal ends of the middle phalanges, and large flexor tubercles on the distal phalanges.

The amount of divergence of the first pedal digit is unknown but its basal articulation (with the entocuneiform) is certainly unlike those of the other digits. The tight saddle articulation probably limited the digit to flexion and extension, there being little opportunity for lateral and medial deviation and probably none for axial rotation.

(vi) Skeletal Restoration

Considering the skeletal adaptations of *P. kummae* in concert, a restoration of the skeleton in a normal standing posture is provided in Fig. 37 and of the whole animals in Fig. 38.

Figure 37. Skeletal reconstruction of *Ptilodus kummae*, n. sp., based principally on UA 9001. Details of the pectoral girdle and forelimbs are uncertain and the skull is based on that of *Ptilodus montanus* (after Simpson, 1937c).

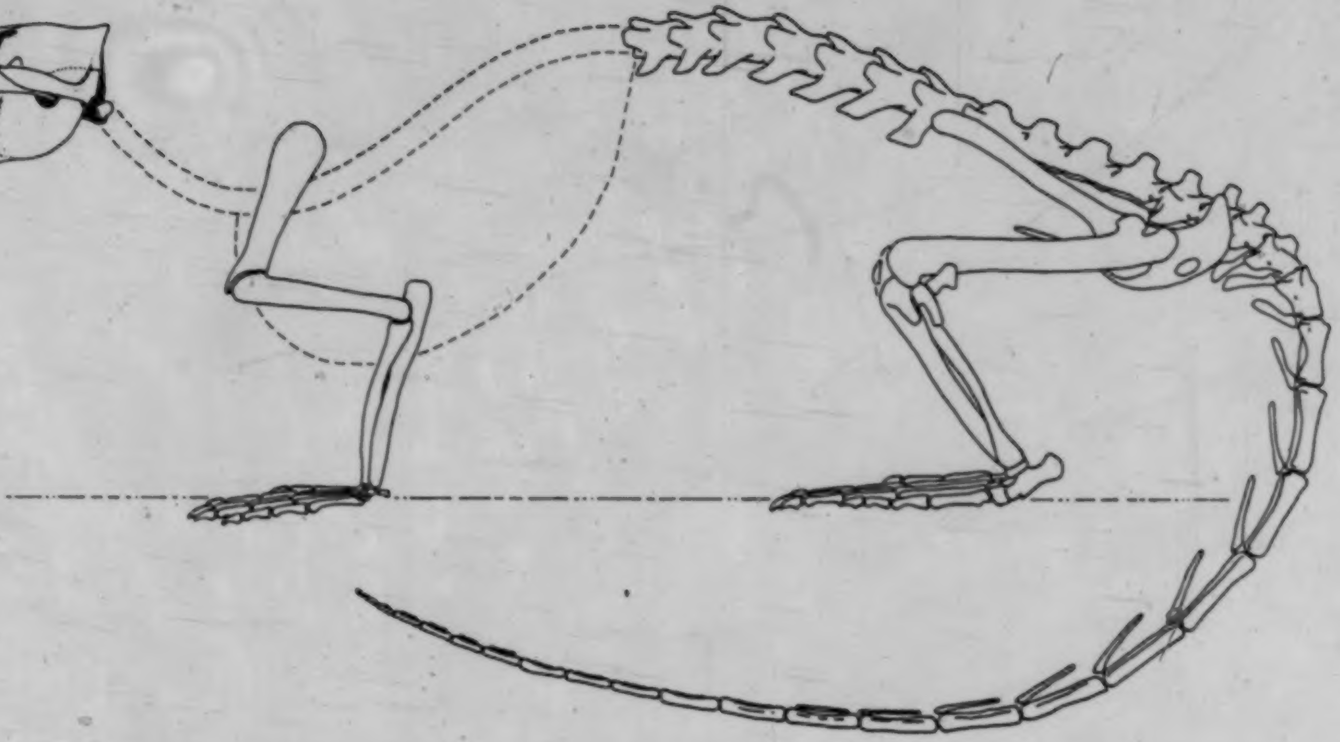
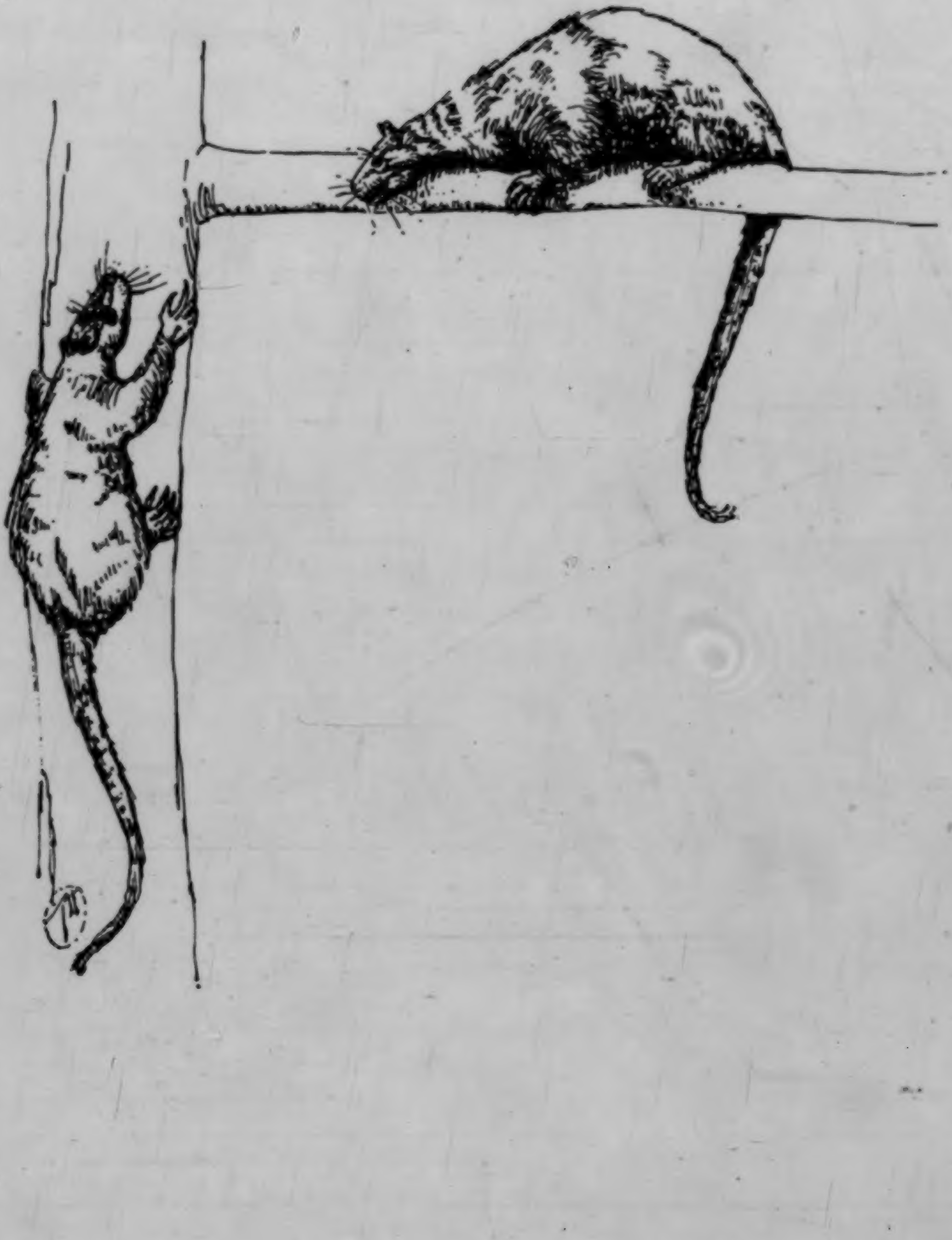


Figure 38. Artist's reconstruction, under the direction of the author, of two individuals of Ptilodus kummae, n. sp.. About two-fifths natural size.



E) Locomotory Habits of Ptilodus kummae

The specimen of Ptilodus montanus described by Gidley (1909) and the specimen of Eucosmodon sp. described primarily by Granger and Simpson (1929) have provided the bases for inferences of locomotory habit in multituberculates. Ptilodus was characterized as saltatorial by Gidley (1909), as it was by Broom (1910, p.767), who stated that Ptilodus was "a ground-hopping animal which was probably quite unable to climb trees."

Simpson (1926) measured the lengths of femora and humeri of many small and medium-sized mammals and concluded that the ratio between the two, the variate employed by both Gidley (1909) and Broom (1910) to suggest a saltatorial habit for Ptilodus, was not particularly discriminatory between saltatorial or cursorial habits and was especially poor in determining if the mammal was terrestrial or arboreal. Simpson (1926) did, however, conclude (p. 247) that Ptilodus "was probably a swiftly moving and agile quadruped" but that (p.249) "to settle the problem as to whether they (multituberculates) were arboreal or terrestrial complete knowledge of the limbs is required, indeed even this might not settle things definitely. It is, however, a fact that they are accompanied in the rocks by abundant evidence of arboreal vegetation and we have seen that they depend in large measure on these trees for their sustenance. It would be remarkable if many of them were not at least semi-arboreal."

Eucosmodon sp. was later depicted by Simpson and Elftman (1928, p.18) as a "chiefly arboreal" mammal, the inference derived from a detailed analysis of its hindlimb musculature and the orientation of its limbs.

Similar conclusions are derived here from the osteological analysis of the almost complete postcranial skeleton (UA 9001) of Ptilodus kummae. In UA 9001, the tibia is considerably shorter than the femur, a ratio that, in itself, clearly indicates that P. kummae was not saltatorial nor highly cursorial. That P. kummae was not cursorial is also inferred from the orientation of the propodial limb segments, which were held oblique to sagittal and, in lateral view, almost horizontally in the normal standing posture. The structure of the humerus, particularly the lack of hypertrophy of the deltopectoral crest, is a clear indicator of non-fossorial habits.

Caution has recently been advocated regarding inferences of locomotory habit from skeletal form. Jenkins (1974b), for example, has emphasized the false dichotomy that exists in views on mammalian arborealism and terrestrialism. Structural adaptations of a small mammal for locomotion in a spatially irregular habitat will not only include adaptations to arboreal activity but to locomotion on almost any uneven substrate. Conversely, an osteological analysis of a mammalian skeleton that results in the inference that the animal was a generalized, non-cursorial quadruped capable of pronation-supination of the forefeet, inversion-eversion of the hind feet, considerable flexibility of the vertebral column, etc., does not necessarily imply a strictly arboreal habit. Structural and physiological adaptations to spatially discontinuous and uneven surfaces have been elucidated in detail by Jenkins (1971b, 1974b) and Jenkins and Parrington (1976).

A tail exceeding the length of the head and body is commonly found in arboreal or saltatorial mammals (Dagg, 1973). That Eucosmodon sp. was not saltatorial (or fossorial) has been shown by Simpson and Elftman (1928) and, owing to basic similarities in structure, the same inference can be applied to P. kummae. However, although the length and robustness of the tail seem to indicate a primarily arboreal habit for P. kummae, it should be noted that the structure of the tail is not always dictated by locomotory requirements (see summary of other functions in Dagg, 1973).

That P. kummae was at least capable of progression in an arboreal milieu is strongly suggested by the highly mobile limbs, a flexible vertebral column, and an exceedingly long and heavy tail. Cartmill (1972, expanded in 1974) has evinced considerable evidence that the possession of well developed claws (as in P. kummae) on the hands and feet of small arboreal mammals is particularly adaptive for "clinging to or climbing on thick trunks and branches, ...running along horizontal supports, hanging beneath slender supports, leaping from tree to tree, and many other activities" (1974, pp.62-63). Grasping extremities and reduced claws of similarly sized mammals are particularly suited for well-controlled progression on supports of small diameter. If these inferences hold true, one would expect that *P. kummae* was not a common inhabitant in shrubs or in the terminal branches of the canopy.

As a working hypothesis, albeit a conservative one, *P. kummae* may be characterized as an herbivorous, small, prototherian mammal that possessed a locomotory repertoire adapted to a partly, if not strictly, arboreal habitat.

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